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New Species of the Earthworm Genus *Anisochaeta* (Oligochaeta: Megascolecidae) from New South Wales

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ABSTRACT. The number of *Anisochaeta* from New South Wales is more than doubled to 50 species in the present account. Twenty-seven species are newly described, one of which is tentatively attributed to the dubious genus *Propheretima*. A checklist is presented with the distributions of the twenty-three previously described *Anisochaeta* from NSW that were variously attributed to the genera *Perichaeta, Megascolex*, and *Spenceriella*. One species, *Megascolex crateroides* Boardman, 1943, is herein synonymized with *Anisochaeta gracilis* (Fletcher, 1886b). A replacement name, *Anisochaeta trichaeta*, is proposed for the homonym of the Victorian *Trichaeta australis* Spencer, 1900. A key is provided for currently known NSW species.

The generic definition of *Anisochaeta* is modified to accommodate forms with the newly discovered vesiculate nephridial condition. Several of the new species have setae between the male pores, further reducing the distinctiveness of *Propheretima* from the prior genus *Spenceriella*, which is itself currently synonymized under *Anisochaeta*.

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The current study was instigated under the biodiversity "Hot Spots" project at the Australian Museum to work on unidentified material held in their earthworm collection. The emphasis was on unidentified material in samples from State Forests and Reserves in the northeast region of NSW (mostly collected by Ed Easton in March–May, 1983), but various other specimens from around the State were also examined.

Anisochaeta, widespread throughout the southern states of Australia, appears from the current study to be particularly diverse in the New England region of NSW. One sample of 35 specimens from New England National Park consisted of ten new taxa. Although most NSW species appear highly localized, some have acquired greater ranges via fluvial or human-mediated transportation. Thus *A. exigua murrayana* (Fletcher, 1887a) occurs from the Riverina region of NSW and Victoria to near the mouth of the Murray River in South Australia, *A. tenax* (Fletcher, 1886b) from Sydney has been reported from the Marquesas Islands, in the South Pacific (Michaelsen, 1900: 226), while *A. sebastiani* (Blakemore, 1997b) occurs in southern Queensland and Tasmania as well as in NSW (Blakemore, 1997b: 1838).

The present paper reports on the Australian genus *Anisochaeta* Beddard, 1890 (as recently restored by Blakemore, 1997a: 1822–1824) into which most of the native species that were at one time placed in *Megascolex, Perichaeta, Trichaeta, Spenceriella*, and *Gemascolex* are now transferred. Previously known *Anisochaeta* species are attributed to Fletcher who, in a series of papers (1886–1890), described a total of about 69 species and varieties, including 26 belonging to *Perichaeta*. These *Perichaeta* comprised 16 species and six varieties (total 22 taxa) from NSW, six species from Queensland, and two species each from South Australia and Victoria. Other authors documented *Anisochaeta* species from various Australian states. Spencer (1893, 1895, 1900) described, respectively, 22 (*Perichaeta*) species from Victoria plus one from South Australia, six species from Tasmania, and ten species (as *Trichaeta* and *Megascolex*) from Victoria and Queensland. Michaelsen (1907a,b, 1916) described 22 *Megascolex* species; these were, respectively, eight species (six previously known) from Victoria, South Australia, and NSW; 11 from Western Australia; and three from Queensland. Jamieson (1974b) listed 11 *Spenceriella* and *Gemascolex* species as occurring in South Australia but apparently overlooked the two *Anisochaeta* species and varieties from South Australia described by Fletcher (1890: 1552).

Methods and abbreviations

Most material examined was collected by Ed Easton, but unfortunately his survey methods are unknown. In particular it is not known whether he disregarded exotic species if he came upon them, nor is it known how intensively he sampled at any one locality. The exact location of some sites is also unresolved, especially one recorded on labels as "Face Fern Valley, New England National Park". This park has no "Face Fern Valley", but Tree Fern Valley (G.R. 430261—Ebor 1:25,000 sheet 9337–2–5) in the Point Lookout Section at the west of the New England National Park, is the most likely location (information courtesy of M. Dwyer, NSW Park and Wildlife Service, Dorrigo District). However, about 30 km east on the boundary of the Bellinger River National Park, is Ferny Face ridge (G.R. 753360—Darkwood 1:25,000 9437–3–5). The former location is considered the most likely as Easton's next sampling was further west at Cathedral Rock National Park. Thus, throughout the following text, the label locality "Face Fern Valley" is changed to Tree Fern Valley.

Following Michaelsen's (1900) method, segments are counted from the anterior using the normal and more familiar Arabic numerals (to avoid the confusion inherent in use of Roman numerals), intersegments are designated by a slash (e.g., 3/4), variations shown by a comma, and range by a dash (e.g., 3,4–5). Setae, counted from the ventral-most on each side, have lower case italic letters (e.g., *a, b, c*); setal lines refer to longitudinal setal series. Right- and left-hand-sides are rhs and lhs, respectively. Gut contents are described to give an indication of the ecological strategies of feeding and burrowing. New South Wales is abbreviated to NSW. All examined material is preserved in 80% ethanol and lodged in the Australian Museum, Sydney (with registration beginning AM W) and in the National Earthworm Collection of the CSIRO Division of Entomology, Canberra (ANIC). Locality data are set off with quotation marks when copied from original labels; Australian Map Grid coordinates are prefixed AMG and are derived from maps. Dorsal dissections were performed under magnification, specimens were pinned on a wax tray containing ethanol and sketched using a *camera lucida*.

Figure 1 is annotated thus: acc. gl.—accessory glands; amp.—spermathecal ampulla; clit.—clitellum (shown shaded); diva.—spermathecal diverticulum (often iridescent); d.p.—dorsal pores; g.m.—genital markings; neph.—nephridium; neph. bla.—nephridial bladder; peri.—peristomium (= first segment, lacks setae); pr.—prostatic gland (ducting to male pore); pro.—prostomium (above mouth); sept.—septa; sp.—spermathecae (opening at spermathecal pores). All scale bars are 1 mm. Holotypes, paratypes and non-type specimens are identified in the text by the upper case abbreviations: H, P and S.

Systematics

Anisochaeta Beddard, 1890

Anisochaeta Beddard, 1890: 56.–Blakemore, 1997b: 1822–1824.
Trichaeta Spencer, 1900: 30–31.
Spenceriella Michaelsen, 1907b: 160–161.–Jamieson & Wampler, 1979: 639.
Gemascolex Edmonds & Jamieson, 1973: 23–24.–Jamieson, 1974b: 87.

Diagnosis. Perichaetine (i.e., more than eight setae per segment), at least in the mid- and hind-body. Female pores single or paired on 14. Male pores from tubuloracemose or racemose prostates paired on 18. An oesophageal gizzard in 5 or 6. Nephridia meroic (i.e., more that one pair per segment), at least in the fore-body, avesiculate or vesiculate, often tufted in the anterior. Spermathecae one or more pairs (sometimes unpaired), with one or more extramural diverticula. Calciferous glands and intestinal typhlosole present or absent, intestinal caeca and gizzards absent. Modified penial setae present or absent. Segmental and intersegmental genital markings present but sometimes reduced or absent.

Type species. *Perichaeta coxii* Fletcher, 1886a.

Distribution. Australia, all states, and New Zealand (Lee, 1959: 279).

Remarks. See Blakemore (1997b) for a recent discussion on this genus. The diagnosis is modified to include vesiculate meroic nephridia, as several species in the current study (*A. aemula* n.sp., *A. lavatiolacuna* n.sp., *A. toonumbari* n.sp., *A. yabbratigris* n.sp.) were found to have nephridial bladders. This condition also occurs in the Australian genus *Cryptodrilus* Fletcher, 1886a and the Oriental genus *Pleionogaster* Michaelsen, 1892 (see Blakemore 1997c: 1686–1689, for discussion of these two genera). The possibility of creating a new genus for these vesiculate forms

(as currently used to differentiate the lumbricine genera *Cryptodrilus* and *Notoscolex*) is deferred pending phylogenetic analysis of respective taxa.

Some of the species newly described below have pharyngeal tufted nephridia and either have or lack calciferous glands; intraspecific variations in paired or unpaired female pores are also noted. Moreover, intrasegmental genital markings are reported for several species that are clearly assignable to *Anisochaeta* (e.g., species described by Spencer, 1893, Michaelsen, 1907a, and in *Trichaeta australis* Spencer, 1900). These observations remove the only remaining justification for the genus *Gemascolex*, as noted by Blakemore (1997b: 1823–1824), and reinforce synonymy of this genus with *Anisochaeta*.

Checklist, with distributions, of previously described *Anisochaeta* species from New South Wales

Several of Fletcher's species have type material that is not traceable, but there is a possibility some specimens remain unrecognized in parts of the Fletcher Collection donated to the Australian Museum.

1 *Perichaeta attenuata* Fletcher, 1889: 1552–1555; *Anisochaeta attenuata*.–Beddard, 1890: 56; *Megascolex attenuatus*.–Michaelsen, 1900: 216. From Mt Wilson. (Type AM W1343).

2 *Perichaeta australis* Fletcher, 1886a: 561–565, figs. 9–11; 1886b: 956–957; 1887a: 399; *Megascolex australis*.–Michaelsen, 1900: 222–223. From Burrawang and Sydney (Mt Wilson specimens were transferred to *Perichaeta monticola* Fletcher, 1887a). (Syntypes missing).

> Transfer of Victorian *Trichaeta australis* Spencer, 1900 to Anisochaeta, makes this a junior secondary homonym of *Anisochaeta australis* (Fletcher, 1886a). Under article 60 of the ICZN the replacement name: *Anisochaeta trichaeta* **n.nom.** is proposed here for Spencer's species.

3 *Perichaeta austrina* Fletcher, 1886b: 956–957, fig. 5; 1887a: 399; 1890: 1001–1002; *Megascolex austrinus*.–Michaelsen, 1900: 223; 1907a: 16–17. From Burrawang, Sydney and (Michaelsen) Blue Mountains between Mt Victoria and the Jenolan Caves region. (Syntypes missing).

4 *Megascolex celmisiae* Jamieson, 1973: 242–246, figs., 5C, 6H, 7F, table 2. From Mt Kosciuszko. (Types: H, P1–20, AM W4662–2682).

> The description by Sims & Gerard (1985: 136, fig. 49) of specimens introduced from NSW to Strathclyde, Scotland, that they identify as "*Spenceriella minor* (Spencer, 1900)", appears to more closely match *Anisochaeta celmisiae*. These two species usually have, respectively, two and three pairs of spermathecae, although Jamieson (1973: 246) noted that a spermatheca was missing from 7 in one of the two dissected specimens of *A. celmisiae*. Moreover, the figure in Sims & Gerard (1985, fig. 49) has some indication of erasure of a third pair of spermathecal pores in intersegment 6/7.

5 *Perichaeta coxii* Fletcher, 1886a: 565–569; 1889: 1554; *Anisochaeta coxii*.–Beddard, 1890: 56; *Megascolex coxi*.–Michaelsen, 1900: 216. From Mt Wilson. (Syntypes missing).

6 *Perichaeta enormis* Fletcher, 1889: 1555–1556; *Anisochaeta enormis*.–Beddard, 1890: 56; *Megascolex enormis*.–Michaelsen, 1900: 215–216. From Gosford region. (Syntypes missing).

7a *Perichaeta exigua* Fletcher, 1887a: 387–389; *Megascolex exiguus*.–Michaelsen, 1900: 225. From Springwood (Blue Mountains) Randwick and Manly Beach (near Sydney). (Type AM W1347).

7b *Perichaeta exigua* var. *murrayana* Fletcher, 1887a: 389; 1889: 1552; *Megascolex exiguus* var. *murrayana*.–Michaelsen, 1900: 225. From Mulwala on the Murray River, NSW, and (Fletcher, 1889: 1552) from the shores of Lake Alexandrina, South Australia. (Syntypes missing, South Australian material reported by Fletcher from "Adelaide Museum" [sic]).

> On the information available, *Anisochaeta exigua murrayana* probably merits specific status. Reynolds & Cook (1976: 142) erroneously list synonymies of the latter taxon under *Amynthas* and *Pheretima*.

8 *Perichaeta fecunda* Fletcher, 1887a: 401–402; 1890: 1003–1004, 1007–1008; *Megascolex fecundus*.–Michaelsen, 1900: 225, 234. From Mt Wilson and Lawson in the Blue Mountains (Types: AM W1346).

> Fletcher (1890: 1007–1008) described a possibly distinct variety of *Anisochaeta fecunda* (Fletcher, 1887) from Burrawang that is, nevertheless, similar to his "Variety b" of *Anisochaeta macleayi* (Fletcher, 1889) as noted by (Fletcher, 1890: 1005–1006), also from Burrawang. Fletcher (1889: 1550–1551) further described one species, and its varieties, as *Perichaeta indissimilis*, from Lake Alexandrina, South Australia, that also appears closely allied to *A. fecunda*.

9 *Megascolex fletcheri* Michaelsen, 1907a: 21–22, figs. 14–15. From the Jenolan Caves region of the Blue Mountains. (Syntypes, Hamburg Museum 6889, and AM W3432).

10 *Perichaeta gracilis* Fletcher, 1886b: 958–960 (non *Perichaeta gracilis* Bourne, 1887); *Megascolex gracilis*.–Michaelsen, 1900: 220; *Megascolex crateroides* Boardman, 1943: 174–176, figs. 4–5, **n.syn.** From Auburn near Parramatta and (Boardman) Mt George in the Jenolan Caves region. (Type, AM W3320; Boardman's specimen is AM W3320).

> *Megascolex crateroides* is here synonymized with *Anisochaeta gracilis* as there are no appreciable differences between the specimen described by Boardman and Fletcher's previous description.

11 *Perichaeta hamiltoni* Fletcher, 1887a: 399–401; *Megascolex hamiltoni*.–Michaelsen, 1900: 234. From beside Cudgegong River, Guntawang. (Types, AM W1349).

12 *Megascolex jenolanensis* Boardman, 1943: 176–178, figs. 6, 7. From the Jenolan Caves region. (Types, AM W3317–3319).

13 *Perichaeta macleayi* Fletcher, 1889: 1556–1558; 1890: 1003–1007; *Megascolex macleayi*.–Michaelsen, 1900: 223; *Spenceriella macleayi*.–Blakemore & Elton, 1994: 251–154, fig. 1. Type locality is Sydney, also from Mt Victoria in the Blue Mountains, Raymond Terrace, Morpeth, Coonabarabran and from the banks of the Namoi at Gunnedah; reported from Richmond (Blakemore & Elton, 1994) and Deniliquin in the Riverina region, NSW (Barley & Kleinig, 1964); now known also from Broulee, Oolong, Book Book (near Wagga Wagga), NSW, and Churchill and Yea, Victoria (Blakemore, unpub.). (Syntypes, AM W1344–1345).

Fletcher (1890) described three varieties and three sub-varieties of *Anisochaeta macleayi* (Fletcher, 1889). Whereas *c* sub-varieties (from Mt Victoria, Raymond Terrace, Morpeth, Coonabarabran and Gunnedah) agree tolerably on information given, varieties *a* and *b* (from Mt Wilson, Lawson and Burrawang) differ considerably. Thus all varieties may not be conspecific.

14 *Perichaeta macquariensis* Fletcher, 1890: 1000–1002; *Megascolex macquariensis*.–Michaelsen, 1900: 224. From the banks of the Macquarie River at Dubbo. (Syntypes: AM W972, AM W976, AM W977).

15 *Megascolex mediaeviae* Michaelsen, 1907a: 19–21, fig. 13. From Blue Mountains, between Mt Victoria and Jenolan Caves near *Halfway* guesthouse. (Syntypes, Hamburg Museum HM V6900).

16 *Perichaeta monticola* Fletcher, 1887a: 390–391; *Perichaeta australis* (part.) Fletcher, 1886a: 565; *Megascolex monticola*.–Michaelsen, 1900: 223; 1907a: 16, fig. 11; Boardman, 1943: 170–173, fig. 3. From Blue Mountains, Mt Wilson (type locality) to the Jenolan Caves region. (Neotype, AM W1390).

Boardman (1943: 173) describes a variety of this taxon.

17 *Perichaeta raymondiana* Fletcher, 1887a: 398–399; *Megascolex raymondianus*.–Michaelsen, 1900: 224. From Raymond Terrace on the Hunter River. (Syntypes missing).

18 *Megascolex rodwayi* Stephenson, 1931: 53–55, fig. 8; Boardman, 1943: 173–174. From Hampton (type locality) and the Jenolan Caves region. (Syntypes, Natural History Museum, London, BMNH 1930:2.7.4–6).

19 *Anisochaeta sebastiani* Blakemore, 1997b: 1836–1838, fig. 17. From Taringa (Queensland), Launceston (Tasmania) and Broulee (NSW). (Types: ANIC RB.94.16.1-2, Queen Victoria Museum, Launceston, 14:3475).

20 *Perichaeta tenax* Fletcher, 1886b: 953–957, fig. 4; 1890: 1014–1015; *Perichaeta albida* Michaelsen 1892; *Megascolex tenax*.–Michaelsen, 1900: 226. From Auburn near Parramatta (type locality), County of Cumberland and Springwood in the Blue Mountains; and (Michaelsen) from "Marquesas de Mendoza?". (Types: missing according to Reynolds & Cook [1976: 178]).

21 *Megascolex wiburdi* Boardman, 1943: 168–170, figs. 1–2. Mt George in the Jenolan Caves region. (Types: AM W3309–3310).

22 *Perichaeta wilsoniana* Fletcher, 1887a: 400–401; *Megascolex wilsonianus*.–Michaelsen, 1900: 234; *Megascolex willsonianus* [sic].–(*lapsus*) Michaelsen, 1907a: 17. From Mt Wilson and (Michaelsen) the Jenolan Caves region. (Types: AM W1350).

The following key treats species from NSW, both new and known. In addition to the characters given in the generic diagnosis, many species have a ventrally cleft peristomium, setae often increasing in number posteriorly, last hearts in 12, paired ovisacs in 14, and intestinal origin in or near 16. However, some species have exceptions to some of these states. Intraspecific variation is occasionally found in the female pore (single or double), in the exact commencement of dorsal pores, in the duplication of spermathecal diverticula, and in the extent of the development of an intestinal typhlosole—suggesting that these latter characters may be less reliable for separation of some taxa.

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Key to *Anisochaeta* (and *Propheretima*) species in New South Wales

For confirmation, keyed specimens must be compared with species-descriptions because it is probable that many undescribed species await discovery.

1 One pair of spermathecal pores 2

—— Two pairs of spermathecal pores 3

—— Three pairs of spermathecal pores 36

—— Four pairs of spermathecal pores 47

—— Five pairs of spermathecal pores in *cd* lines; calciferous glands absent ..... *A. lavatiolacuna* n.sp.

2(1) Four or five pairs of calciferous pouches in 9,10–13; seminal vesicles in 11 and 12 ..... *A. exigua exigua* (Fletcher, 1887a) and varieties

—— Calciferous arrangement similar [default interpretation of Fletcher]; seminal vesicles in 9 and 12 ..... *A. exigua murrayana*

3(2) Calciferous glands absent 4

—— Calciferous glands present 25

4(3) Spermathecal pores in *a* or *ab* lines 5

—— Spermathecal pores in or lateral to *b* lines 9

5(4) Seminal vesicles in 12 only 6

—— Seminal vesicles in 9 and 12 7

6(5) 17 setae per segment anteriorly; genital markings single, midventral in 18 ..... *A. fletcheri*

—— 8 setae per segment anteriorly; genital markings paired in 18 or single, midventral in 17 and 19 ..... *A. mediaeviae*

7(5) Genital markings in 17 and 19 paired more widely than male pores 8

—— Genital markings in 17 and 19 closely paired or midventral ..... *A. flava* n.sp. and varieties

8(7) Spermathecal pores just median of *a* lines; prostates S-shaped ..... *A. angusticlavia* n.sp.

—— Spermathecal pores in *ab* lines; prostates bilobed ..... *A. conspecta* n.sp.

9(4) Spermathecal pores mostly in *b* lines 10

—— Spermathecal pores lateral of *b* lines 19

10(9) Anterior genital markings in 10 and/or 11 form 88-like tetrad 11

—— Anterior genital markings unpaired, mid-ventral or non-tetrad pair 13

11(10) Tetrad markings in 10 and 11 median of *a* lines ..... *A. novaeanglica* n.sp.

—— Tetrad markings in 10 or 11 in *ab* lines 12

12(11) Tetrad markings in 10; spermathecal diverticula as long as ampullae ..... *A. wiburdi*

—— Tetrad markings in 11; spermathecal diverticula shorter than ampullae ..... *A. ima* n.sp.

13(10) Anterior markings unpaired, mid-ventral 14

—— Anterior markings paired 15

14(13) Anterior markings in 10 and/or 11 sucker-like ..... *A. toonumbari* n.sp.

—— Anterior markings in 9–11,12 button-like discs ..... *A. bulla* n.sp.

15(13) Spermathecal diverticula extend beyond ampulla 16

—— Spermathecal diverticula shorter than ampulla 17

16(15) Small size (about 35 mm); female pore single; gizzard weak; nephridia vesiculate ..... *A. aemula* n.sp.

—— Moderate size (70–90 mm); female pores paired; gizzard strong; nephridia avesiculate ..... *A. tunicata* n.sp.

17(15) Small size (about 35 mm); first dorsal pore 5/6; no markings on 17; nephridia reduced ..... *A. paucula* n.sp.

—— Moderate size (75–150 mm); first dorsal pore 3/4/5; markings in 17 and 19 at least 18

18(17) Size 75–90 mm; setae evenly spaced; markings on 17 postsetal ..... *A. ancisa* n.sp.

—— Size 120–150 mm; setae *bc* > *ab*; markings in 17 presetal ..... *A. rodwayi*

19(9) Spermathecal pores in *b-c* lines 20

—— Spermathecal pores lateral of *c* lines 23

20(19) Setae about 60 per segment; seminal vesicles in 11 and 12 ..... *A. calpetana* n.sp. (part)

—— Setae 20–44 per segment; seminal vesicles in 9 and 12 21

21(20) Accessory markings absent or reduced; gizzard rudimentary; typhlosole absent ..... *A. sebastiani*

—— Accessory markings well developed; gizzard large; typhlosole present 22

22(21) Anterior markings irregular in outline, absent from 17; spermathecal ampullae finely corrugated ..... *A. liberalis* n.sp.

—— Markings disc-like anteriorly, present on 17; spermathecae smooth, elongate ..... *A. calvasaxea* n.sp.

23(19) Spermathecal pores in *c-e* lines 24

—— Spermathecal pores in *g* lines ..... *A. virgata* n.sp.

24(23) First dorsal pore 5/6; markings absent from 19; flaps over male pores ..... *A. garilarsoni* n.sp.

—— First dorsal pore 3/4/5; markings in 19; male pores on penes ..... *A. aterpaenulata* n.sp.

25(3) Calciferous glands (or lateral pouches) six pairs in 8–13 26

—— Calciferous glands (or lateral pouches) two to four pairs 28

26(25) First dorsal pore 10/11; spermathecal diverticula paired ..... *A. enormis*

—— First dorsal pore 12/13; spermathecal diverticula unpaired 27

27(26) Seminal vesicles 11 and 12; last hearts 13 ..... *A. coxii*

—— Seminal vesicles 9 and 12; last hearts 12 ..... *A. attenuata*

28(25) Calciferous glands (or lateral pouches) four pairs 29

—— Calciferous glands or pouches two or three pairs 31

29(28) Anterior markings form 88-like tetrad in 10; calciferous glands 10–13 ..... *M. monticola*

—— Markings not tetrad; calciferous glands or pouches in 10–13 or 11–14 30

30(29) Setae 60; first dorsal pore 5/6; spermathecal pores in *bc*; calciferous pouches paired in 10–13; seminal vesicles in 11 and 12 ..... *A. calpetana* n.sp. (part)

—— Setae 24–32; first dorsal pore 3/4/5; spermathecal pores in *a* lines; calciferous glands paired extramural in 11–14; seminal vesicles in 9 and 12 ..... *A. erica* n.sp.

31(29) Calciferous glands three pairs 32

—— Calciferous glands in two segments 34

32(31) Anterior markings 88-like tetrad in 9 and 10; spermathecal pores in *b,c*; calciferous glands paired in 11–13 ..... *A. tenax*

—— Anterior markings absent or not tetrad; spermathecal pores lateral of *d* 33

33(32) Large size (c. 145 × 9 mm); spermathecal pores in *f*; accessory genital markings absent; setae absent between male pores; calciferous glands paired 10–12 ..... *A. australis*

—— Moderate size (100 × 3 mm); spermathecal pores in *de*, genital markings numerous; setae between male pores; calciferous glands paired 11–13 ..... *Propheretima monsmonitionis* n.sp.

34(31) Spermathecal pores in *a* lines; gizzard weak; calciferous glands annular in 13 and 14 ..... *A. palustris* n.sp.

—— Spermathecal pores in *b,c* lines; gizzard large; calciferous glands paired in 11 and 12 35

35(34) Spermathecal pores in *b* lines; genital markings in (9) 10 and 11 disc-like ..... *A. filix* n.sp.

—— Spermathecal pores in *c* lines; markings in 10 and/or 11 with eye-like pores ..... *A. macleayi* and varieties

36(1) Calciferous glands absent 37

—— Calciferous glands present 41

37(36) Spermathecal pores in *ab* lines 38

—— Spermathecal pores lateral of *b* lines 39

38(37) Genital markings pore-like in *ab* in 10, pore-like or ridges lateral to male pores; typhlosole absent ..... *A. celmisiae*

—— Markings disc-like in *bc* in 9 and 10, none lateral on 18; typhlosole present ..... *A. rava* n.sp.

39(37) Spermathecal pores in *c-d* lines; genital markings absent from anterior, present in 19; no setae between male pores ..... *A. lata* n.sp.

—— Spermathecal pores in *d-f* lines; markings in anterior present or absent, present on 18 or 17 and 19; setae between male pores 40

40(39) Spermathecal pores in *d-e* lines; markings in anterior absent, paired on 18; gizzard large; intestinal origin 17 ..... *A. gracilis*

—— Spermathecal pores in *e-f* lines; markings in 7 and 8, 17 and 19; gizzard weak; intestinal origin 16 ..... *A. yabbratigris* n.sp.

41(36) Calciferous glands four or five pairs in 10–13,14 42

—— Calciferous glands three pairs in 10–12 43

42(41) Size < 100 mm; penial setae absent; calciferous glands 10–13 ..... *A. wilsoniana*

—— Size 130–180; penial setae present; calciferous glands 10–13,14 ..... *A. macquariensis*

43(41) Size < 100 mm; anterior genital markings in 10 or 9,10 rectangular 44

—— Size > 100 mm; anterior markings absent, midventral or paired in 10 or 9,10 45

44(43) Spermathecal pores in *a* lines; genital marking unpaired midventral in 16, 17, 19–20,21 (not 18); first dorsal pore 3/4/5; intestinal origin 15 ..... *A. rubeospina* n.sp.

—— Spermathecal pores in *b* lines; genital marking paired in 17, 19 and in 18 median to male pores; first dorsal pore 5/6; intestinal origin 16 ..... *A. austrina*

45(43) Genital markings paired in 10 or 9,10 and 16,17 and 19 (not 18); setae in anterior *aa* = 4 *ab* ..... *A. chani* n.sp.

—— Anterior markings wanting, swollen or thickened ventrally in 17 and 18 often with paired papillae; setae in anterior *aa*>2*ab*<4*ab* 46

46(45) Setae 24–36; in anterior dorsal setal gap = 2 *ab*, ventral setal gap slightly wider ..... *A. raymondiana*

—— Setae 16–30; in anterior dorsal setal gap = 4 *ab*, *aa* not quite so wide ..... *A. hamiltoni*

47(1) Size < 80 mm; spermathecal pores in *b* lines; first dorsal pore in 4/5; calciferous pouches in 10–14; last hearts 13 ..... *A. fecunda*

—— Size > 100 mm; spermathecal pores in *ab* lines; first dorsal pore in 5/6; calciferous glands paired in 10–13; last hearts 12 ..... *A. jenolanensis*

Anisochaeta aemula n.sp.

Fig. 1

Material examined. HOLOTYPE: AM W24544, (H), Washpool State Forest, NSW, c. 29°16'S 152°22'E, collected 9.iii.1992, M. Gray & P. Croft, pit trap sample set 22.ii.1992, "17CM Trap 3 FN 5082" (mature, figured and dissected). PARATYPES: none. The original sample contained 2 immature specimens that could not be positively identified as this species.

External features. Length 35 mm. Width: about 1.5 mm. Segments: 70. Colour: uniform buff in alcohol, clitellum light brown. Prostomium: open epilobous; peristomium ventrally cleft. Clitellum: ½13–16. Dorsal pores: small in 4/5, larger from 5/6. Setae: 24 on segments 12 and 20, 26–28 per segment posteriorly. Nephropores: lateral pores at anterior of segments near *h* lines, especially obvious on clitellum. Spermathecal pores: 7/8/9 in *b* setal lines. Female pore: single on 14. Male pores: on 18 in *ab* lines at centre of flat eye-like papilla. Genital markings: whole ventral aspect of 10 and 11 tumid to *d* lines with paired presetal sucker-like discs embedded at anterior of segments in *b* lines; on 17 paired wide pads postsetal in *ab* lines co-joined posteriorly by tumid rim; on 19 similar pads presetal in *bc* lines within circular rims.

Internal anatomy. Septa: none especially thickened. Gizzard: rudimentary or weakly muscular, barely wider than oesophagus in 6. Oesophagus: dilated most in 11–13 but not calciferous, narrows in 15. Nephridia: vesiculate meroic, tubules clustered ventrally in 5 and 6 (not definitely tufted) then spread laterally with about 5 or 6 tubules per side and with small bladders in series laterally on each side (whether connecting with one or more tubules indeterminate), nephridia smaller after clitellum but bladders persist. Vascularization: dorsal vessel single onto pharyngeal mass in 4; hearts 10–12 increasingly large and connected to supra-oesophageal vessel. Spermathecae: paired in 8 and 9, ampulla spherical on equally long duct with long clavate diverticulum. Male organs: holandric, seminal vesicles racemose in 9 and 12, iridescent testes and funnels in 10 and 11. Ovaries: in 13 sheet-like with several egg strings; small stalked ovisacs paired in 14. Prostates: flattened tubuloracemose (almost racemose) in 18–19, duct narrow; penial setae absent. Large sessile glands, probably associated with genital markings, present ventrally in 17 and 19 (see Fig. 1). Intestine: from 16; typhlosole absent; gut contents organic matter and dark topsoil.

Remarks. *Anisochaeta aemula* exemplifies the vesiculate condition of the genus. Lateral excretory bladders (vesicles) associated with the nephridia have not been previously recognized in *Anisochaeta* species although they are found in several species in the current account (see *A. lavatiolacuna, A. toonumbari, A. yabbratigris*). *Anisochaeta aemula* is distinguished from superficially similar species of the genus *Perionychella*, as the latter have holoic nephridia (one pair per segment), with or without bladders. Presence of nephridial bladders in species of these two genera may be homoplasic, or indicative of retention via common ancestry, whereby the meroic condition in *Anisochaeta* is an apomorphy. Alternatively, the acquisition of nephridial bladders may be autapomorphic within *Anisochaeta*. Testing of these possibilities by molecular or cladistic analysis is beyond the resources of the current study.

Anisochaeta aemula resembles *A. flava* (also from the Washpool site which itself resembles *A. wiburdi*) and *A. ancisa*. Apart from nephridial bladders, the distinguishing characters of *A. aemula* are the distribution of its genital markings, weak gizzard, spermathecal diverticula longer than ampullae, and the large glands in 17 and 19 that possibly have a secretory function associated with the genital markings on these two segments.

Etymology. *Aemulus*: rivalling, jealous—a reference to its resemblance to *Perionychella* species.

Distribution and habitat. Washpool State Forest, sympatric with *Anisochaeta flava, A. garilarsoni* and *A. lavatiolacuna*. Numerous unidentifiable (damaged or immature) *Anisochaeta* specimens were obtained from these Washpool samples, but no other earthworm genera were present. Pit trap collection indicates that this species is active on the surface of the soil. The weak digestive system, organic matter in the intestine, and nephridial bladders for moisture regulation, also suggest that this species is a topsoil or litter dweller.

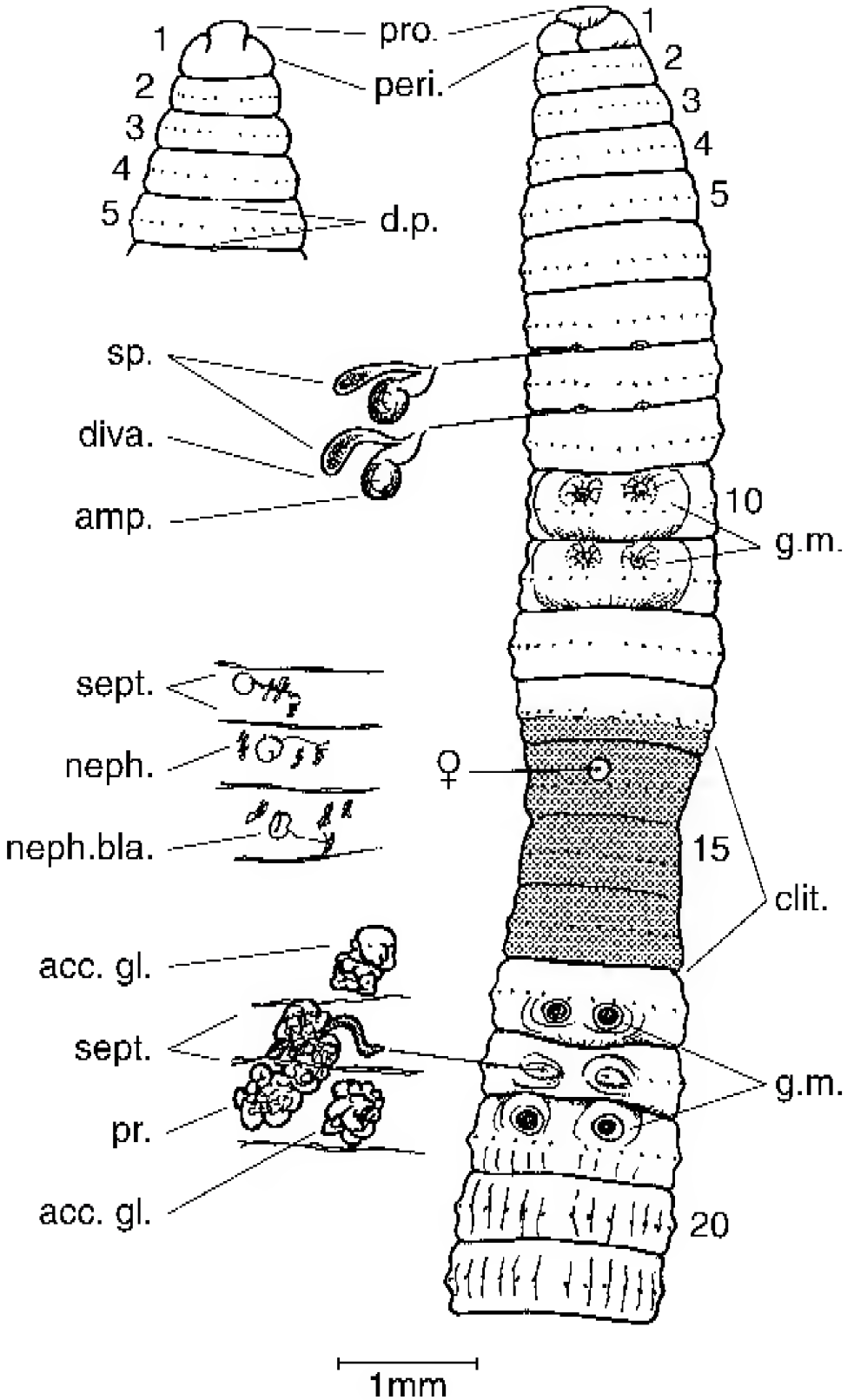

Figure 1. *Anisochaeta aemula* ventral view of holotype with dorsal view of prostomium, spermathecae, nephridial arrangement on lhs in segments 13–15, accessory glands in 17 and 19, and lhs prostate in 18–19.

Anisochaeta ancisa n.sp.

Fig. 2

Material examined. HOLOTYPE: AM W24470, (H), label reads: "Face Fern Valley, New England National Park, NSW" [probably Tree Fern Valley—see above], c. 30°30'S 152°30'E, 17.iii.1983, Ed Easton, "Jar 15 Sp 31" (mature, figured and dissected). PARATYPES: ANIC RB.98.2.25, (P1), same details as H (mature, dissected); AM W24471, (P2), same details as H (mature); ANIC RB.98.2.26, (P3), same details as H (aclitellate mature, dissected).

External features. Lengths (mm): 85 (H), 90 (P1), 80 (P2), 75 (P3). Width: about 2.5 mm. Segments: 108 (H), 120 (P1). Colour: anterior and dorsum dark brown with violet iridescence and darker mid-dorsal line, clitellum orange. Prostomium: open epilobous tapering; peristomium ventrally cleft. Clitellum: ½13–16. Dorsal pores: small in 3/4, open from 4/5 (occluded on clitellum). Setae: 24 on 12 and 20, 34 posteriorly. Nephropores: not found. Spermathecal pores: 7/8/9 centred in *b* lines within tumid lips that extend almost from *a* lines to *c* lines. Female pore: single (in H, P2), closely paired on 14 (in P1, P3). Male pores: on apices of large dome-shaped mounds that are deeply sunken within common ventral field on 18. Genital markings: on 8 (in P1 only), paired sucker-like discs presetal and centred in *b* lines, on 10 similar paired discs (all specimens), on 11 smaller paired discs centred on *a* lines (all specimens); on 17 paired circular pads postsetally centred in *a* lines within common sunken pit that extends almost to *c* lines; on 19 oblique presetal dark pits that taper from line of male porophores to the centre of the mid-ventral setal gap where they are almost confluent. Sunken male field and markings in 17 and 19 occur in all specimens.

Internal anatomy. Septa: none especially thickened. Gizzard: muscular but compressible barrel in 5. Oesophagus: not especially dilated, widest in 13, valvular in 15. Nephridia: avesiculate meroic, not tufted but tubules numerous and larger in anterior, no funnels found. Vascularization: dorsal vessel single; hearts 10–12 connected to weak supra-oesophageal vessel that runs 8,9–12,13. Spermathecae: paired in 8 and 9, ampulla compressed along its axis to be as wide or wider than it is long, tapering duct with medium sized diverticulum near its exit. Male organs: holandric, seminal vesicles large racemose in 9 and 12, iridescent testes and funnels in 10 and 11. Ovaries: in 13 long egg strings; paired ovisacs in 14. Prostates: flattened tubuloracemose in 18–19, duct muscular; penial setae absent. Intestine: from 16; typhlosole absent; gut contents organic soil with few grits.

Remarks. *Anisochaeta ancisa* differs from *A. rodwayi*—firstly, in the distribution of genital markings, described by Stephenson "as small, round, darker spots" on 10, 11, and 16 and 17 (presetally), as well as and on 19–21 (in *A. ancisa* the markings on 17 are postsetal); secondly, on its tufted nephridia in segments 3–5. Boardman (1943: 173–174) provides additional data on variation within *A. rodwayi* that reinforce these differences from *A. ancisa*.

Species that resemble *Anisochaeta ancisa* in the present account are *Anisochaeta conspecta* and *Anisochaeta flava*.

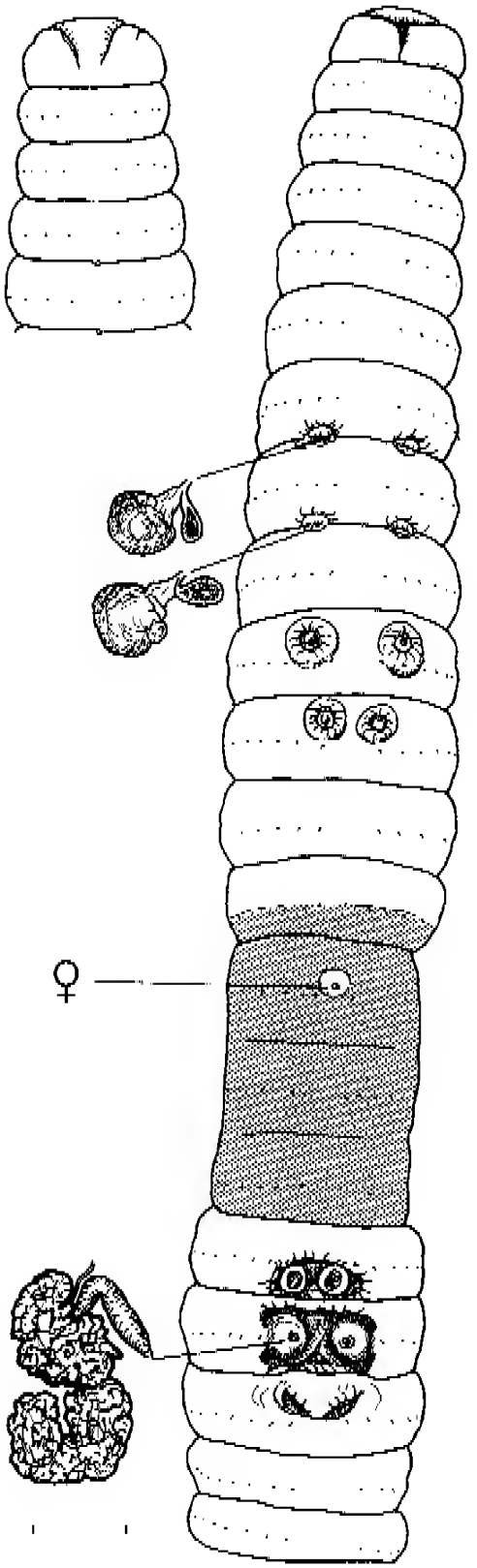

Figure 2. *Anisochaeta ancisa* ventral view of holotype with dorsal view of prostomium, spermathecae and lhs prostate in 18–19.

Similar markings in 10 and 11, are found in *A. conspecta* but it has more extensive markings on, and after, the clitellum as well as spermathecae and prostates that both differ in shape and more ventral openings. *Anisochaeta flava* perhaps comes closest to the current species, but has anterior markings on segments 9 or 10 only, tends to have fewer setae, more widely paired female pores and tufted nephridia. Additional distinctive characters of *A. ancisa* are the prominent spermathecal pores, and the male porophores and markings in adjacent segments which are emphasized by surrounding hollow depressions.

Etymology. *Ancisus*: cut round—for the markings around the male pores.

Distribution and habitat. Tree Fern Valley—found in association with several other congeners (i.e., *A. filix, A. lata, A. liberalis, A. novaeanglica, A. paucula, A. tunicata, A. virgata*; see also *A. bulla* varieties). It is perhaps especially in such situations of high diversity, where mate recognition is crucial, that closely related species can be separated on variations in genital markings.

Anisochaeta angusticlavia n.sp.

Fig. 3

Material examined. HOLOTYPE: AM W24550, (H), Yabbra State Forest, NSW, c. 28°30'S 152°40'E, collected 2.iv.1992, M. Gray & D. Charley, pit trap sample set 15.iii.1992, "2BG Trap 19 FN 5118" (mature, figured and dissected). PARATYPES: ANIC RB.98.2.54, (P1), same location as H but "Trap 13 FN 5112" (mature, dissected); AM W24551, (P2), same details as P1 (mature); ANIC RB.98.2.55, (P3), same location as H but collected 15.iii.1992, pit trap set 27.ii.1992, "Trap 13 FN 5102" (mature, dissected); AM W24552, same details as P3 (mature); ANIC RB.98.2.56, same details as P3 (mature); AM W24553, (P6, P7), same details as P3 (two matures, one aclitellate); AM W24557, (P8), same location as H but collected 15.iii.1992, pit trap sample set 27.ii.1992, "Trap 19 FN 5108" (mature).

External features. Lengths (mm): 65 (H), 80 (P1), 58 (P2), 80 (P3), other specimens 38–65. Width: about 2.5 mm. Segments: 110 (H), 104 (P1), 95 (P2). Colour: in alcohol, anterior dorsum puce with darker mid-dorsal line, after clitellum pigment fades except for this line which continues to tail; clitellum buff. Prostomium: open epilobous parallel; peristomium ventrally cleft. Clitellum: ½13–16. Dorsal pores: from 4/5. Setae: 20 on 12 and 20, only one or two setae added further posteriorly. Nephropores: not found. Spermathecal pores: 7/8/9 within small puckered lips just ventral of setal *a* lines. Female pores: paired on 14. Male pores: on 18 on flat pads (with what looks like small pore-like dimples near male pores) approximately in *ab* lines and within raised and yellow tumid field that fills ventral aspect of 18 and extends to *d* lines. Genital markings: on 10 and 11, small paired and confluent discs in *ab* presetally (all specimens except H and P7, where only occur on 11, and P8 where absent); on 17 widely paired discs approximately in *c* lines within common tumid and elongate mainly postsetal pad; on 19 similar arrangement as in 17, but presetal, plus more median paired discs in *bc* lines postsetally that overhang 19/20. Paired markings within raised pads present in 17 and 19 in all specimens, P2–P7 have extra pair presetally in 17 (mirroring those in 19).

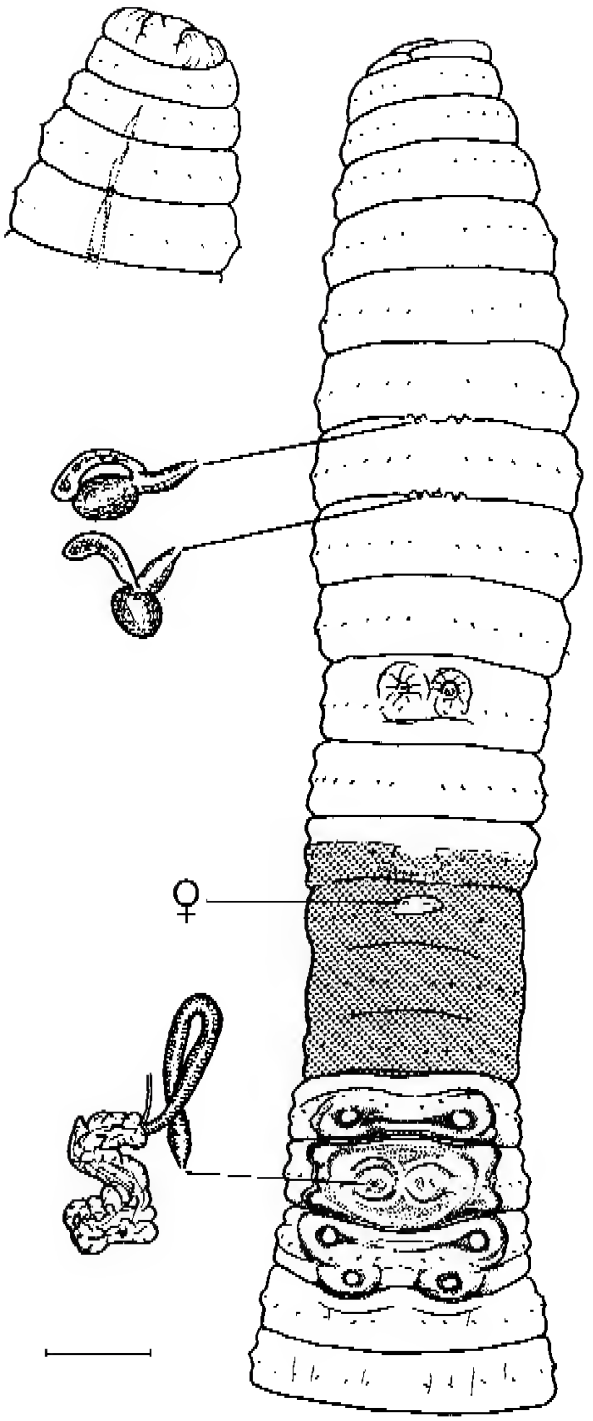

Figure 3. *Anisochaeta angusticlavia* ventral view of holotype with dorsal view of prostomium, spermathecae and lhs prostate in 18–19.

Internal anatomy. Septa: 9/10–11/12 only slightly thickened. Gizzard: muscular barrel in 5. Oesophagus: dilated and vascular in 8–14,15 (except where compressed by seminal vesicles in 9 and 12), appears transitional to intestine in 15. Nephridia: avesiculate meroic, tufted in 5–6, then as several small tubules per side, especially fine after clitellum. Vascularization: dorsal vessel single; hearts 10–12 from supra-oesophageal vessel that runs 9–14. Spermathecae: paired in 8 and 9, ampulla spherical on equally long narrow duct with diverticulum that attaches at the junction of ampulla and duct and curves beyond ampulla. Male organs: holandric, seminal vesicles large, racemose in 9 and 12, iridescent testes and funnels in 10 and 11. Ovaries: in 13 with long egg strings; paired ovisacs in 14. Prostates: flattened tubuloracemose in 18–19, duct long, narrow and folded back on itself; penial setae absent. Intestine: origin in 16; typhlosole absent; gut contents fine yellow soil with some organic debris and grits.

Remarks. Characteristics of *Anisochaeta angusticlavia* are the widely paired, prominent and often symmetrical genital markings in 17 and 19, spermathecal pores ventral in setal *a* lines, and the distinctively long prostate ducts and spermathecal diverticula. Morphologically it resembles several other quadrithecal species in the current account that lack calciferous glands but may have tufted nephridia in the anterior, differing from these by the points just noted. Spermathecal pores in setal *a* lines are met with in Michaelsen's *A. fletcheri* and *A. mediaeviae*, but both differ on other points, especially having seminal vesicles in 12 only.

Etymology. *Angusticlavia*: "wearing a narrow purple stripe", referring to the mid-dorsal line.

Distribution and habitat. Yabbra State Forest, from pit trap samples. Other species obtained from this location were *A. calpetana, A. yabbratigris*, and one variety of *A. bulla* (see descriptions below) plus several other specimen of *Anisochaeta* and *Digaster* spp. that were either too immature or in insufficient numbers for adequate description.

Anisochaeta aterpaenulata n.sp.

Fig. 4

Material examined. HOLOTYPE: AM W24497, (H), Bald Rock National Park, NSW, c. 28°51'S 152°03'E, 28.iii.1983, Ed Easton, "Jar 36 Sp 49" (mature, figured and dissected). PARATYPES: ANIC RB.98.2.43, (P1), same details as H (mature, dissected); AM W24498, (P2), same details as H (aclitellate mature, dissected); ANIC RB.98.2.44, (P3), same details as H (subadult); AM W24499, (P4–P8), same details as H (5 specimens: juveniles and immatures that agree superficially); ANIC RB.98.2.45, (P9), same location as H except "Jar 37 Sp 49 100 m from base of Bald Rock" (mature).

External features. Lengths (mm): 75 (H, P1, P2), 65 (P3), 42–65 (P4–P8), 70+ (P9). Width: about 3 mm. Segments: 98 (H, P1). Colour: anterior dorsum iridescent black with darker mid-dorsal line, after clitellum pigment sooty brown except for this line which continues to tail, ventrum and intersegments

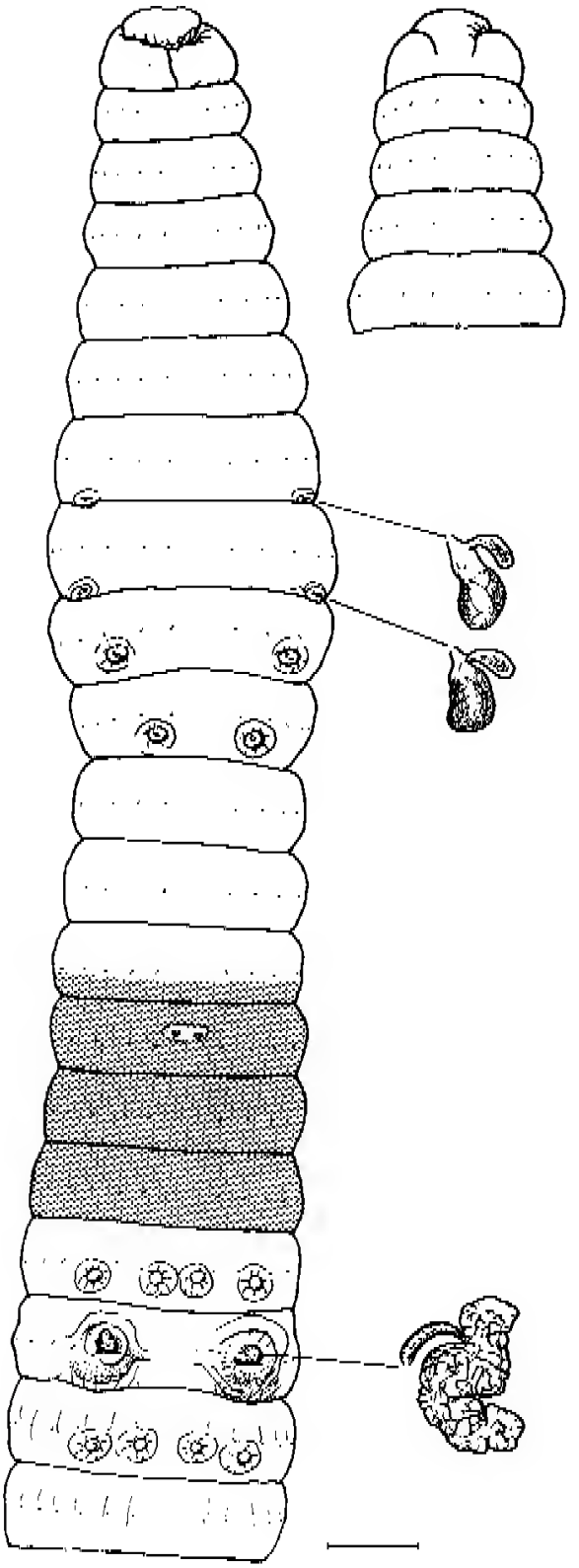

Figure 4. *Anisochaeta aterpaenulata* ventral view of holotype with dorsal view of prostomium, spermathecae and rhs prostate in 18–19.

pale; clitellum tan. Prostomium: wide open epilobous; peristomium ventrally cleft. Clitellum: ½13–16. Dorsal pores: small in 3/4, larger from 4/5 (continuous on clitellum). Setae: 22 on 12, 26 on 20, up to 40 posteriorly. Nephropores: lateral pores at anterior of segments seen from 5, in *g* or *h* lines in anterior, with other less obvious pores at anterior of segments and equatorial near some setae. Spermathecal pores: 7/8/9 widely paired with large apertures just lateral of *d* lines. Female pores: paired on 14. Male pores: on 18 at centre of largish pads that extend from *a* to *c* lines within copulatory chambers on tip of small penes eversible from roof of chambers (no setae intervene between male pores). Genital markings: all postsetal, widely paired white-centred sucker-like discs median of *c* lines on 9 (on H only); similar more median discs approximately in *ab* lines on 10 (all other mature specimens); on 17 two pairs of discs one pair in *bc*, one pair median in *aa* (only the outer couple present in P2, there are three median discs on 17 in P9); on 19 markings similar to those on 17 are repeated (only outer couple present in P2). Markings are consistently in 10, 17 and 19.

Internal anatomy. Septa: 7/8–11/12 only slightly thickened. Gizzard: moderately muscular in 5, only slightly larger than oesophagus in 6. Oesophagus: not especially dilated (calciferous glands absent). Nephridia: avesiculate meroic, not tufted in anterior but dense clusters ventrally to 9 then migrate laterally to approximately at anterior and posterior of most setae; no structures found corresponding to lateral nephropores (i.e., no bladders); funnels not found. Vascularization: dorsal vessel single; hearts 10–12 from weak supra-oesophageal vessel. Spermathecae: paired in 8 and 9, ampulla tapers to duct, medium sized clavate diverticulum ectally. Male organs: holandric, seminal vesicles racemose in 9 and, larger, in 12, testes and funnels in 10 and 11 (iridescent only in 11). Ovaries: in 13 as sheets terminating in several egg strings; paired ovisacs in 14. Prostates: flattened tubuloracemose in 18–19 from moderately muscular duct; penial setae absent. Intestine: origin in 16; typhlosole absent; gut contents organic matter.

Remarks. Previously known *Anisochaeta* species from NSW which, like *A. aterpaenulata*, have 2 pairs of spermathecae in 7/8/9 and lack of extramural calciferous glands are *A. fletcheri* and *A. mediaeviae, A. rodwayi, A. sebastiani* and *A. wiburdi*. These species differ from *A. aterpaenulata*, not least, by having spermathecal pores more ventral in *a, b* or *c* setal lines and, where present, by their genital markings. In the present account, *A. garilarsoni* and *A. virgata* are morphologically similar, and all three species are darkly pigmented. However, *A. garilarsoni* lacks markings in 19 and has dorsal pores from 5/6; while *A. virgata* has presetal markings in 10 and 19 (i.e., opposite to *A. aterpaenulata*), intestinal origin apparently in 15, and longer spermathecal diverticula. Characteristics of *Anisochaeta aterpaenulata* are widely paired spermathecal pores in *d* lines, distinctive arrangement of the genital markings postsetally in (9), 10, 17 and 19, and the male pores on small penes.

Etymology. *Aterpaenulata*: "cloaked in black" for its distinctly dark colouration.

Distribution and habitat. Bald Rock National Park (see also *A. calvasaxea* and *A. ima*). Dark body pigmentation and organic matter in intestine suggests that this species is active on the surface layer of soil.

Anisochaeta bulla n.sp.

Fig. 5

Material examined. HOLOTYPE: AM W24459, (H), Cathedral Rock National Park, NSW, c. 30°25'S 152°15'E, 18.iii.1983, Ed Easton, "Jar 18 Sp 8" (mature, possible posterior regenerate, figured and dissected). PARATYPES: ANIC RB.98.2.20, (P1), same details as H (mature, dissected); AM W24460, (P2), same details as H (mature, dissected); ANIC RB.98.2.21, (P3), same details as H (mature); AM W24461, (P4), same details as H (mature); AM W24462, (P5–P11), same details as H (7 specimens: 4 aclitellate matures, one damaged plus 3 juveniles). (The original sample also contained 4 or 5 other specimens, plus fragments, that were either too damaged or too immature to allow adequate description).

Non-type material. AM W24466, (S1), Tree Fern Valley, New England National Park, NSW, c. 30°30'S 152°30'E, 17.iii.1983, Ed Easton, "Jar 15 Sp 31" (mature, one of several specimens, dissected); AM W24473, (S2), same details as S1 (subadult, dissected); AM W24458, (S3), Grafton—Glen Innes Road, 19.iii.1983, Ed Easton "Jar 26 Sp 27?/31?" (mature, dissected, one of seven specimens—the others being three apparently different *Anisochaeta* spp. that were either aclitellate or otherwise unsuitable for adequate description).

External features. Body of H tapers to tail, other specimens have slightly spade-shaped tails. Lengths (mm): 82+ (H), 100 (P1), 85 (P2), 90 (P3), 95 (P4). Width: about 3 mm. Segments: 110+ (H), 149 (P1), 109 (P2). Colour: pale unpigmented in alcohol, clitellum buff. Prostomium: open epilobous; peristomium ventrally cleft. Clitellum: 14–16 and encroaching slightly onto adjacent segments. Dorsal pores: small in 3/4, open from 4/5. Setae: 16 on 12, 20 on 20, 16–28 posteriorly; setae well spaced ventrally and more crowded dorsally, occasional setae missing in anterior. Nephropores: not found. Spermathecal pores: 7/8/9 in or near *b* lines. Female pores: paired on 14. Male pores: on 18 on small mounds in *ab* that are sunken in crescentic troughs. Genital markings: four in 9–12 (H, P1, P4–P6, S2) or three in 9–11 (P2, P3, P7–11, S1, S3) midventral sucker-like discs in tumid mounds that extend to setae *a*; ventral aspect of 18–19 tumid to *c* lines with three small papillae lateral to male pores on 18 plus several smaller papillae just below the line of 17/18 and 18/19 corresponding with interval between male papillae (all specimens, but the distribution of the papillae around the male pores varies somewhat).

Internal anatomy. Septa: 7/8–11/12 only slightly thickened. Gizzard: large muscular barrel in 5, displaced to occupy ½7 to ½9 (i.e., two segment lengths). Oesophagus: not especially dilated (calciferous glands absent), narrow and valvular in 15. Nephridia: avesiculate meroic, tufted in 5–7 then spread equatorially with about 20 small discrete tubules per side. Vascularization: dorsal vessel single; hearts

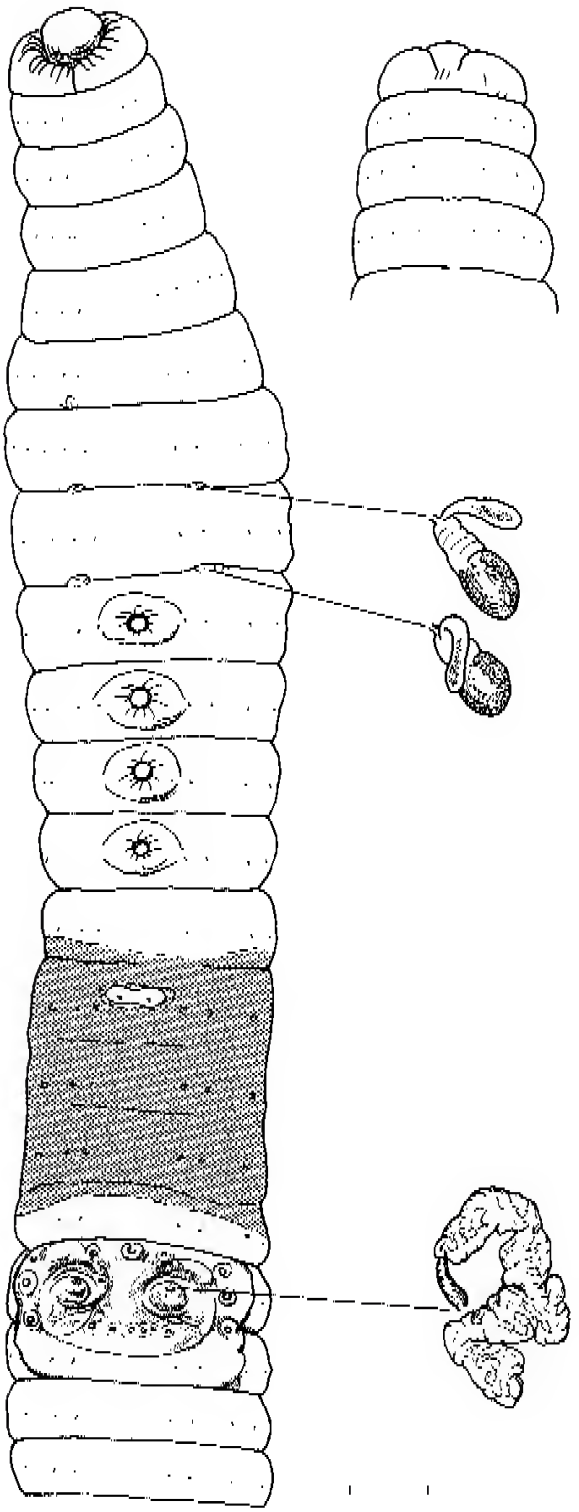

Figure 5. *Anisochaeta bulla* ventral view of holotype with dorsal view of prostomium, spermathecae and rhs prostate in 18.

10–12, supra-oesophageal vessel weak. Spermathecae: paired in 8 and 9, saccular ampulla on almost equally wide duct, medium sized clavate diverticulum ectally; ampulla, duct and diverticulum all approximately same length. Male organs: holandric, seminal vesicles racemose saccular in 9 and elongate in 12; testes and funnels iridescent in 10 and 11. Ovaries: in 13 long and feather-like; paired ovisacs in 14. Prostates: flattened tubuloracemose in 18–19 from short muscular duct; penial setae absent. Intestine: origin in 16; thin but deeply lamellate typhlosole develops from 20; gut contents sandy organic soil. (Non-type specimens differed internally, S1 and S2 lacked appreciable typhlosole, while S3 had typhlosole but also had four pairs of extramural calciferous glands in 10–13, amongst other differences).

Remarks. The prominent button-like mid-ventral genital markings distinguish *Anisochaeta bulla*. Morphologically it is similar to *Anisochaeta tunicata*, both species have tufted nephridia, a large gizzard, lack calciferous glands and have two pairs of spermathecal pores in *b* setal lines. However, in *A. tunicata* the anterior markings are paired and, further, the spermathecae have different forms.

Several other *Anisochaeta* populations having mid-ventral genital markings similar to those in *A. bulla* were identified, but are unresolved, in the current study. One specimen from Yabbra State Forest (AM W24555), and two specimens from the original sample from Cathedral Rock had two markings in 9–10; five specimens from Gibraltar Range National Park (AM W24568) had five mid-ventral markings in 9–13. As with the non-type material described above, it is not certain that these specimens are attributable to *A. bulla*.

Etymology. *Bulla*: button—for the genital markings.

Distribution and habitat. Cathedral Rock National Park is just west of New England National Park.

Anisochaeta calpetana n.sp.

Fig. 6

Material examined. HOLOTYPE: AM W24563, (H), Twin Bridges, Gibraltar Range National Park, NSW, c. 29°30'S 152°20'E, c. 20.iii.1983, Ed Easton, "3,000' [1,000 m] Jar 27 Sp 8" (aclitellate mature, figured and dissected). PARATYPES: ANIC RB.98.2.59, (P), Yabbra Scrub, Yabbra State Forest, 28°38'S 152°30'E, 12.xii.1988, Smith, Hines, Pugh & Webber, "UNE Focal Peak Survey, Pit Trap Y2" (clitellate mature, darkened and brittle specimen, missing tip of tail, dissected).

External features. Body stout. Lengths (mm): 110 (H), 110+ (P). Width: about 4 mm. Segments: 165 (H), 93+ (P). Colour: anterior and tail gunmetal grey, rest of body dark brown above with faint mid-dorsal line, light brown ventrally; in P clitellum darker. Prostomium: epilobous almost tanylobous with mid-dorsal furrow; peristomium ventrally cleft. Clitellum: in P ½14 to ½17. Dorsal pores: from 5/6. Setae: approximately 60 throughout, small forming almost complete circle with only narrow ventral and dorsal gaps. Nephropores: not found. Spermathecal pores: small in 7/8/9 in *bc* lines. Female pores: small, closely paired on 14. Male pores: on 18 on tumid mounds as transverse slits, setae absent from the hollow between male pores. Genital markings: on 10 presetally a pair of small

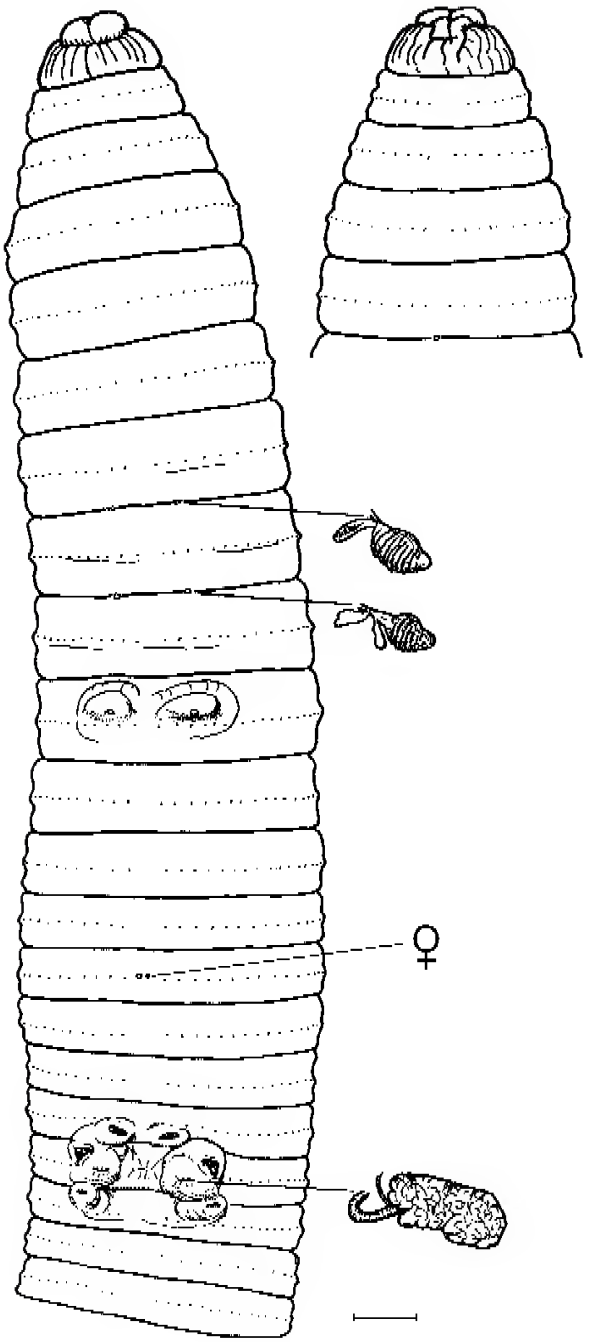

Figure 6. *Anisochaeta calpetana* ventral view of holotype with dorsal view of prostomium, spermathecae and rhs prostate in 18.

discs just anterior to *c* setae on prominent mounds within generally tumid patch that extends laterally and encompasses *f* or *g* lines (only this tumid patch and no discs present in P); on 17 postsetally are paired oblique dark pits in *a* or *b* lines on tumid pads; on 18 paired triangular pits anterolateral to mounds of male pores on tumid pads that encroach on 17/18; on 19 presetally a pair of dark pits in *d-e* lines on tumid pads that encroach on 18/19. For both specimens, the mounds of the male pores and the tumidity of the three adjacent sets of markings are united around the male pores obscuring the intersegmental furrows.

Internal anatomy. Septa: 5/6 thin to base of gizzard, 6/7–11/12/13 increasingly thickened, then thinning. Gizzard: large, muscular barrel in 5. Oesophagus: with paired lateral pouches in 10–13, these pouches are supplied by the supra-oesophageal vessel and have internal lamellae but are not pinched off from the oesophagus so do not form extramural calciferous glands (in H only, in P oesophagus not especially dilated); oesophagus narrows in 14–15. Nephridia: avesiculate meroic, tufting not noted in anterior, numerous parietal tubules that are smaller after the clitellum and closer to the anterior septa although no funnels found. Vascularization: dorsal vessel single onto the pharyngeal mass in 4; hearts 10–12, from moderately developed supra-oesophageal vessel. Spermathecae: paired in 8 and 9, wrinkled, saccular ampulla tapers to duct with medium sized clavate diverticulum ectally, diverticulum may be slightly bifid at tip and one spermatheca had two diverticula on one side. Male organs: holandric, seminal vesicles elongate racemose in 11 and 12 (absent from 9 in H but rudimentary in P); testes and funnels only slightly iridescent in 10 and 11. Ovaries: in 13 composed of fine strings; small paired ovisacs in 14. Prostates: blocky tubuloracemose or racemose in 18 from short muscular duct; penial setae absent but numerous tendons extend from 18 to segments 17 and 19. Intestine: origin in 16; typhlosole absent; gut contents dark organic soil (H) or reddish soil (P).

Remarks. Distinctive characters of *A. calpetana* are the stout, dark body, numerous (about 60) setae per segment, the distribution of its genital markings (paired on 10 and 17–19) and the seminal vesicles in 9, 11 and 12 rather than the more usual 9 and 12. On each of these character, *A. calpetana* differs from *A. cormieri* (Jamieson & Wampler, 1979: 641–644) from Queensland which, nevertheless, it resembles morphologically.

Although oesophageal pouches are noted in the holotype of *A. calpetana* in 10–13 these are not extramural and are not construed as true calciferous glands (this was also the situation in descriptions of *A. rodwayi* and *A. wiburdi*). Supernumerary diverticula are met occasionally in other species (e.g., *A. enormis* and *A. erica* n.sp.).

Etymology. *Calpetana*: "from Gibraltar" (Latin).

Distribution and habitat. Gibraltar Range National Park at 1,000 m and Yabbra State Forest, at the latter location from "dry-subtropical rain forest, sheltered slope 600–900 m". The dark pigmentation, numerous setae (for mobility and protection), gut contents and collection in a pit fall trap suggest that this species is sometimes active on the soil surface.

Anisochaeta calvasaxea n.sp.

Fig. 7

Material examined. HOLOTYPE: AM W24572, (H), Bald Rock National Park, NSW, 28°51'S 152°03'E, 28.iii.1983, Ed Easton, "Jar 36 Sp 31" (mature, figured and dissected). PARATYPES: ANIC RB.98.2.61, (P1), same details as H (mature, dissected); AM W24573, (P2), same details as H (mature); ANIC RB.98.2.62, (P3), same details as H (mature); AM W24574, (34 paratypes), same details as H (34 specimens that agree superficially: 17 matures, 16 aclitellate matures or subadults, 1 immature). (The sample also contained 3 anomalous *Anisochaeta* sp. specimens, AM W24575, that were larger and had different arrangements of genital markings).

External features. Anterior dorsoventrally depressed, tail slightly spade-shaped. Lengths (mm): 100 (H), 110 (P1), 90 (P2), 105 (P3). Width: about 3 mm. Segments: 117 (H), 118 (P1). Colour: uniform buff in alcohol, clitellum brick red. Prostomium: tapering epilobous, almost tanylobous with mid-dorsal furrow; peristomium ventrally cleft. Clitellum: 14–16 and encroaching onto adjacent segments. Dorsal pores: from 4/5. Setae: 20 per segment throughout but some lines irregular posteriorly and odd extra setae added. Nephropores: small pores seen irregularly at anterior of segments in midbody. Spermathecal pores: small in 7/8/9 near *b* lines. Female pores: paired (possibly single on P3) on 14. Male pores: on 18 as narrow lateral slits on darker low mounds that occupy approximately *a-c* lines. Genital markings: on 10 postsetally, and on 11 and 12 presetally, pairs of sucker-like discs approximately in *ab* lines but converging posteriorly; on 17 postsetally and 19 presetally similar paired discs just median to interval of male pores, those in 19 slightly closer together. Markings on 12 often wanting or just an analogue present (in 31 out of 37 specimens) and occasionally a secondary pair of discs are present just posteromedian to *a* setae on 19 (on P2 and two other specimens).

Internal anatomy. Septa: 7/8–12/13 increasingly thickened, then thinning. Gizzard: large muscular barrel mainly in 5 but thin septum 5/6 attaches at about one third of its length and can scarcely be traced to the base, thus it may possibly be partly in 6, displaced to occupy 7 to ½8. Oesophagus: not especially dilated although has longitudinal lamellae on internal surfaces (not calciferous), narrows in 15. Nephridia: avesiculate meroic, tufted in 4–5, then spread laterally as bands of numerous sets of parietal tubules, reduced after clitellum; bladders and funnels not found. Vascularization: dorsal vessel single; hearts 10–12, from weak supra-oesophageal vessel. Spermathecae: paired in 8 and 9, slender ampulla on thin duct with clavate diverticulum ectally, ampulla, duct and diverticulum approximately same length. Male organs: holandric, seminal vesicles racemose in 9 and 12; testes and funnels iridescent in 10 and 11. Ovaries: in 13 as broad sheets with several egg-strings; small paired ovisacs in 14. Prostates: elongate, finely lobulate tubuloracemose in 18, duct long and slender and folded back on itself; penial setae absent. Intestine: origin in 16; deep lamellar typhlosole develops from 20; gut contents dark soil with few grits. No internal glands are associated with genital markings in 17 and 19 as were found in *A. aemula*.

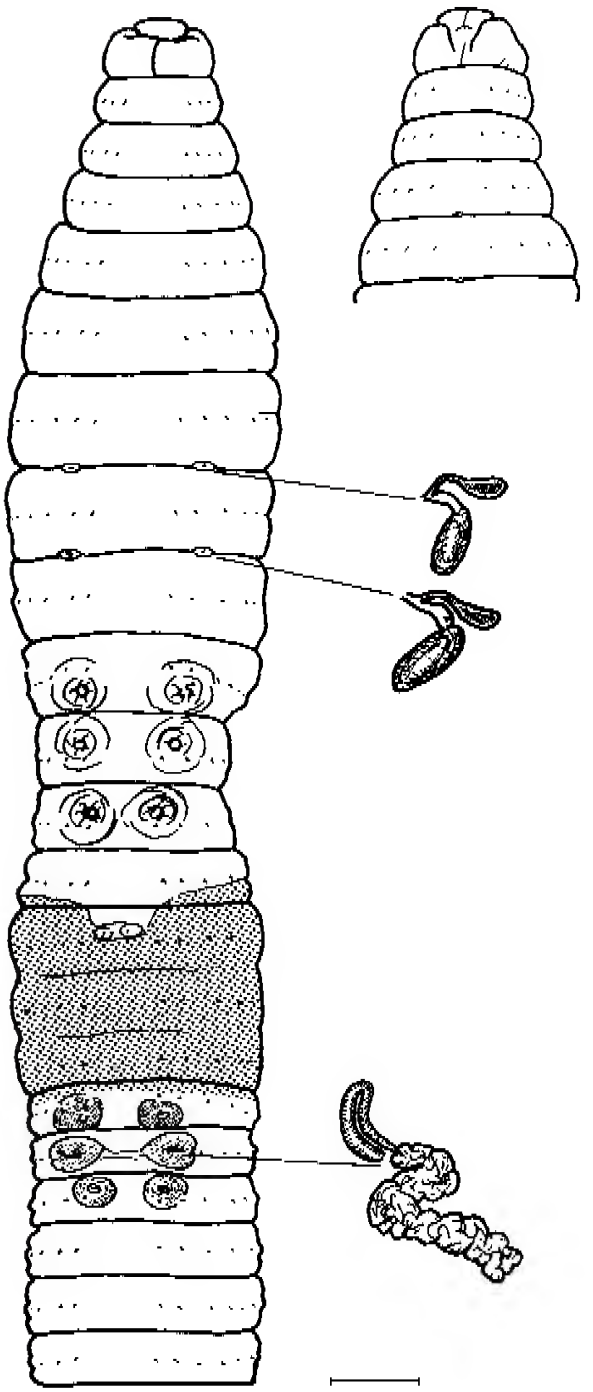

Figure 7. *Anisochaeta calvasaxea* ventral view of holotype with dorsal view of prostomium, spermathecae and rhs prostate in 18–19.

Remarks. The genital markings in *Anisochaeta calvasaxea* resemble those found in *A. aemula, A. flava*, and *A. tunicata*. The markings on 10, however, are postsetal, rather than presetal as in these other species (or more widely paired

than those of *A. flava* variants). Moreover, *A. calvasaxea* further differs from *A. aemula* by having a well-developed gizzard and by lacking nephridial bladders and lacking internal glands in 17 and 19. While the paired markings around the male pores in *A. flava* are midventral and co-joined. The similarity with *A. tunicata* is closer (to the extent that there are 20 setae per segment and the gizzard appears partly in 6 in both species), but this species has more extensive markings on segments 8,9–13 and spermatheca and prostates that are less slender than those found in *A. calvasaxea*.

Etymology. *Calvasaxea*: of bald rock.

Distribution and habitat. Bald Rock National Park (along with *A. aterpaenulata* and *A. ima*).

Anisochaeta chani n.sp.

Fig. 8

Material examined. HOLOTYPE: ANIC RB.98.2.47, (H), Neville nr. Orange, NSW, c. 33°42'S 148°15'E, May 1998, K. Yin Chan, (mature, tip of tail missing, figured and dissected). PARATYPES: AM W24537, (P1), same details as H (mature, tip of tail missing, dissected); ANIC RB.98.2.48, (P2), same details as H (mature); AM W24538, (P3), same details as H (weakly clitellate mature, tip of tail missing, dissected); ANIC RB.98.2.49, (P4), same details as H (aclitellate subadult that lacks genital markings but agrees superficially). ANIC RB.97.3.4, (P5), Cowra, NSW, 9.vii.1992, possibly collected by Nielsen, donated by J.C. Buckerfield, (mature specimen, dissected).

External features. Lengths (mm): 130+ (H), 120+ (P1), 150 (P2), 105 (P3), 90 (P4), 220 (P5). Width: 4–5 mm (P5 7–8 mm). Segments: 160 (P2), 142 (P5). Colour: anterior dorsum dark blue-grey to flanks, whole of ventrum and hind-body pale (with dark mid-dorsal line in P5); clitellum dark (reddish in P5). Prostomium: open epilobous with weak mid-dorsal furrow (more tanylobous in P5); peristomium ventrally cleft. Clitellum: ½13 to ½17. Dorsal pores: small in 4/5, larger from 5/6. Setae: large in anterior, 20 on 12, 28 on 20 and 30–34 towards posterior. Nephropores: not found. Spermathecal pores: obvious in 6/7/8/9 in *ab* but slightly closer to *b* lines. Female pores: paired on 14. Male pores: on 18 at centres of mounds wider than *a* lines surrounded by darker, sunken, dumb-bell-shaped area with tumid lateral borders extending to *c* lines. Genital markings: on 10 two pairs of small markings, one pair just anterolateral to *b* setae, the other pair median and inferior to *ab* on both sides (P5 has an extra pair of small markings just median to setae *a* on 9); in 16 and 17 equatorially merged paired markings, those in 16 median to *aa*, those in 17 slightly wider extending to *a-b* lines; in 19 paired oblique slits or sunken discs within tumid papillae linked by narrow bridge just presetal to *a* setae and median to the line of the male pores.

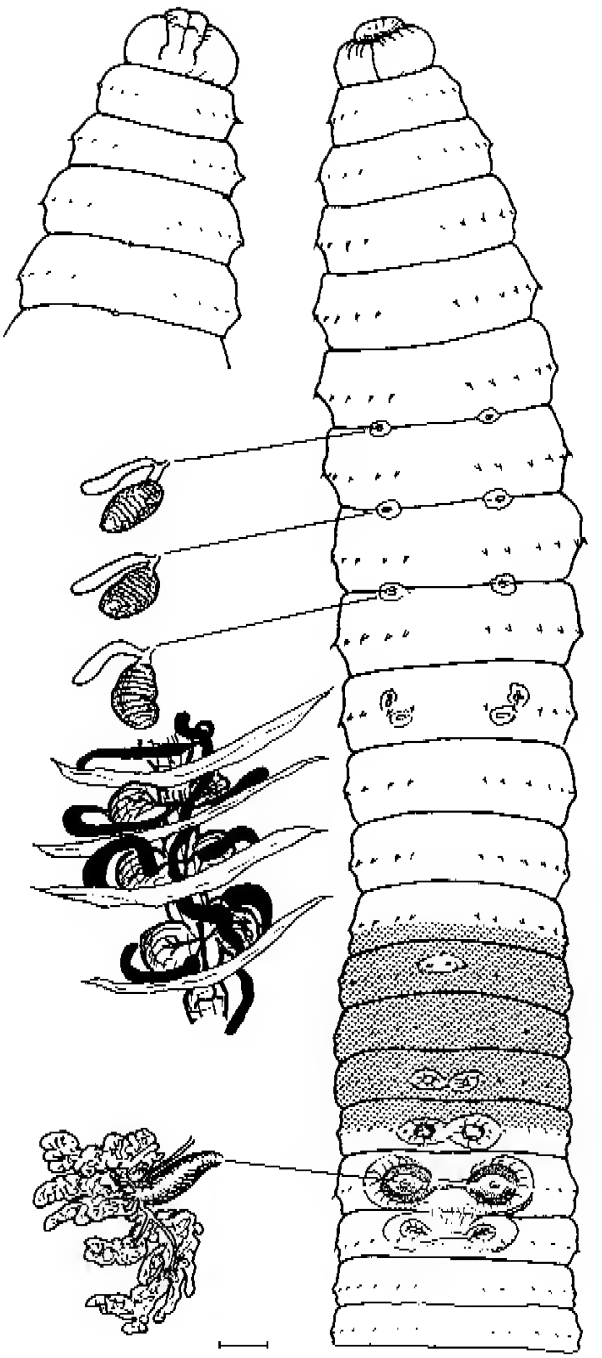

Figure 8. *Anisochaeta chani* ventral view of holotype with dorsal view of prostomium, spermathecae, oesophagus and vascularization in 9–13 showing three pairs of calciferous glands in 10–12, and lhs prostate in 18–19 with externally branching ducts.

Internal anatomy. Septa: 5/6/7/8 displaced rearwards by gizzard, 8/9–12/13 increasingly thick then thinning. Gizzard: large muscular conical in 5 but deflected, corresponding to width of segments 7–8. Oesophagus: lateral extramural calciferous glands paired in 10–12 (three pairs), supplied with blood vessels from supra-oesophageal vessel and lamellate internally with white (calcium) granules; oesophagus narrows in 13–15. Nephridia: avesiculate meroic, tufted in (3)4–5, then spread laterally and reduce in size with bands of numerous (about 15–20 per side) parietal tubules; bladders and funnels not found.

Vascularization: dorsal vessel single onto pharyngeal mass in 3; hearts 10–12 from supra-oesophageal vessel that runs 10 to ½13. (In 10 and 11 at least, hearts connect to the supra-oesophageal vessel with only small connectives to the dorsal blood vessel). Spermathecae: three pairs in 7, 8 and 9; large finely furrowed ampulla on short thin duct joined by clavate diverticulum just longer than the ampulla; (diverticula white rather than iridescent). Male organs: holandric, racemose seminal vesicles elongate and flimsy in 9 and 12; testes and funnels free in 10 and 11, (iridescence not noted). Ovaries: fan-shaped in 13; small paired ovisacs in 14. Prostates: racemose dispersed lobes in 18–19 supplying external ducts that converge, along with vas deferens, at apex of thick muscular duct; penial setae absent; many tendons or muscle fibres fan out from 18 to segments 16–19. Intestine: origin in 16; typhlosole absent; gut contents fine yellow soil (or red sandy soil with many quartz grits in Cowra specimen).

Remarks. Previously known *Anisochaeta* species from NSW with 3 pairs of spermathecae in 6/7/8/9 near *b* lines and 3 pairs of calciferous glands in 10–12, as in *A. chani*, are Fletcher's species *A. austrina, A. raymondiana* and, possibly, *A. hamiltoni*. (*A. rubeospina* in this account, has spermathecal pores in *a* lines).

Fletcher (1886b: 956–957) described sexthecal *Anisochaeta austrina*, comparing it with quadrithecal *A. australis*. Although close morphologically, *A. austrina* differs from *A. chani*, not least, by the anterior genital markings in 9 and 10 being much more prominent and by having an extra pair of papillae median to male pores on segment 18 (see Fletcher, 1886b, fig. 5). Fletcher (1987: 398–400) briefly describes *A. raymondiana* (from Raymond Terrace, Hunter River) and *A. hamiltoni* (from besides the Cudgegong River at Guntawang near Mudgee), comparing them with *A. austrina* (or perhaps he meant *A. australis*). On the information given, they both appear to differ from *A. chani* by having genital markings on 17 and 18 only (i.e., not recorded in 16 nor 19). Further, *A. raymondiana* has narrow mid-dorsal and mid-ventral setal gaps and testis sacs, and *A. hamiltoni*, while having wider setal gaps, has only indistinct swellings on 9 and 10 and also a second pair of papillae (with or without pores) on 18 in addition to papillae with pores on 17 (and 18). (Types of this latter species, AM W1349, were not inspected).

Unique combination of characters in *A. chani* are the large spermathecal pores in 6/7/8/9 in *ab* but perhaps closer to *b* setal lines, the distinctive shape of the spermathecae and multi-lobed prostates, and the distribution of genital markings (on (9),10, 16, 17 and 19). Slight variations are noted for the larger Cowra specimen but as it agrees on most points it is considered to be conspecific.

Etymology. Named in recognition of the collector Dr K. Yin Chan of the New South Wales Department of Agriculture, Wagga Wagga.

Distribution and habitat. Neville township approximately 50 Km south of Orange, and 50 Km north of Cowra. Found "In pasture soil in high numbers" at the former type locality.

Anisochaeta conspecta n.sp.

Fig. 9

Material examined. HOLOTYPE: AM W24560, (H), Richmond Range State Forest, NSW, 28°31'S 152°44'E, c. 27.iii.1983, Ed Easton, "Jar 35 Sp 31" (mature, possibly a posterior regenerate after segment 76, figured and dissected). PARATYPES: ANIC RB.98.2.58, (P1), same details as H (mature, dissected); AM W24559, (P2), same details as H (mature posterior amputee); AM W24561, (P3–P7), same details as H (5 specimens: mature or subadult, several posterior amputees).

External features. Lengths (mm): 85 (H), 100 (P1), 70+ (P2), 70–88 (P3–P7). Width: about 3 mm. Segments: 93+ (H), 104 (P1). Colour: anterior dorsum dark orange-brown with faint blue mid-dorsal line, remainder of body yellowy in alcohol; clitellum orange. Prostomium: open epilobous; peristomium ventrally cleft. Clitellum: ½13–16. Dorsal pores: from 4/5. Setae: 20 per segment for most of body length, increasing up to 30 on caudal segments. Nephropores: small dots noted intersegmentally approximately in line with alternate setal lines. Spermathecal pores: as large curved slits on prominent mounds in 7/8/9 in *ab* but closer to setal *a* lines with ridged arcs surrounding pores. Female pores: paired on 14. Male pores: on 18 as small cruciform slits on opposed mounds that almost meet ventrally within darker rims extending to *b* lines. Genital markings: on 10 and 11 (all specimens) two pairs of circular discs, presetal centred in *ab* lines; on 16 (H and P2 only), 17 (all mature specimens), 19 (H, P1, P2 only), 20 (H, P1, P2, P3 only) and 21 (H, P1, P2, P3 only) large paired postsetal discs approximately in *bc* lines; on 19 (all matures) additional pair of irregular discs encircled by darker rims that are ventrally united by narrow isthmus just anterior to setal arc and just longer than interval of male pores. Thus genital markings of mature specimens are consistently on 10, 11, 17 and presetally on 19.

Internal anatomy. Septa: none especially thickened. Gizzard: large muscular barrel in 5. Oesophagus: dilated and vascularized in 8–14 but not calciferous; narrow in 15. Nephridia: avesiculate meroic, large tufts in 4–6, then dispersed as discrete sets of tubules, about 10 per side, equatorial in forebody, thicker on clitellar segments, small in intestinal segments; bladders, funnels and connections to nephropores not found. Vascularization: dorsal vessel single onto pharyngeal mass in 4; hearts 10–12 from weak supra-oesophageal vessel. Spermathecae: two pairs in 8 and 9; large conical ampulla on short duct joined by medium length clavate diverticulum. Male organs: holandric, racemose seminal vesicles in 9 and 12; testes and funnels in 10 and 11. Ovaries: fan-shaped in 13; small paired ovisacs in 14. Prostates: bilobed, racemose in 18–19, anterior lobe circular, larger posterior lobe folded elongate, both providing external ducts that unite, along with vas deferens at apex of long looped duct; penial setae absent. Intestine: origin in 16; typhlosole absent but low dorsal ridge noted; gut contents gritty topsoil.

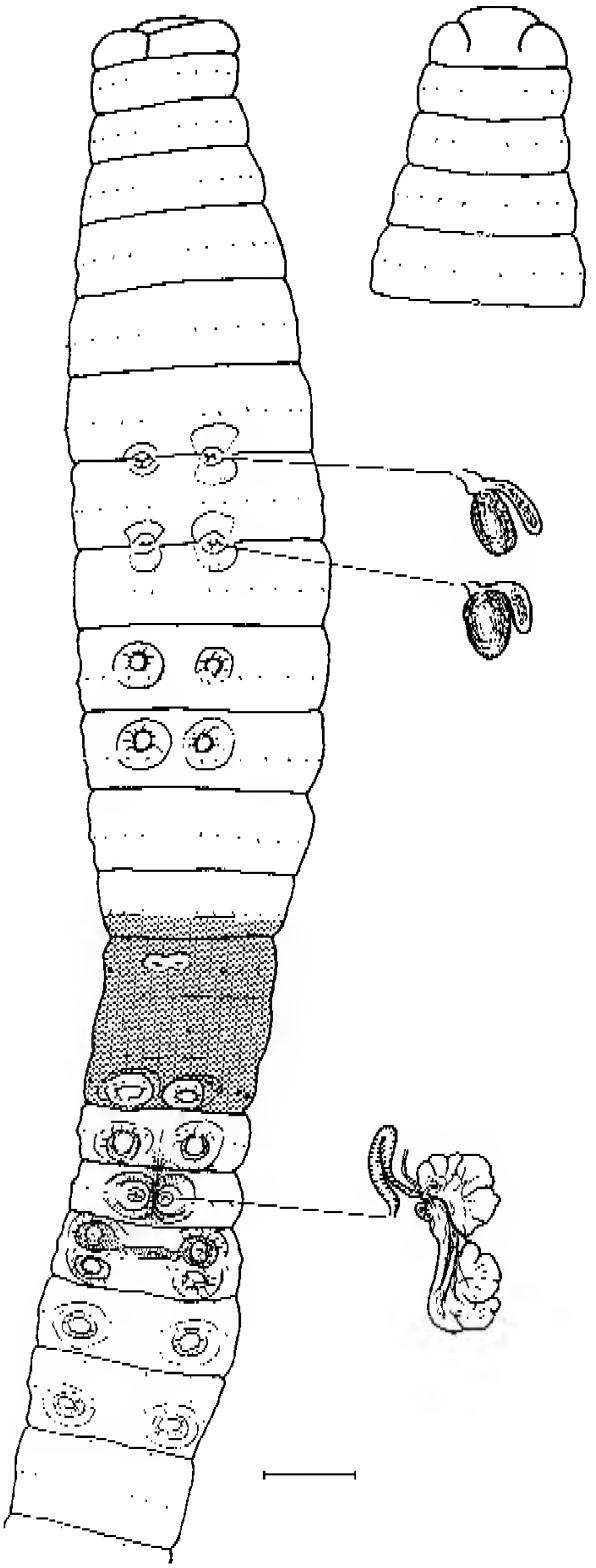

Figure 9. *Anisochaeta conspecta* ventral view of holotype with dorsal view of prostomium, spermathecae, and lhs prostate in 18–19 with externally branching ducts and vas deferens.

Remarks. Features of *Anisochaeta conspecta* are the slit-like male and spermathecal pores, the bilobed racemose prostates, the shape of the spermathecae and the distribution of the genital markings. Especially distinctive is the narrow isthmus linking the glandular markings on the anterior of segment 19. Stephenson's *A. rodwayi* has genital markings, when most abundant, in segments 10,11,16,17,19–21+ (see Boardman, 1943:174 for variations). This distribution is similar to that in *A. conspecta*, however, the markings in *A. rodwayi* are always placed anterior of the setal ring and are more closely paired: either confluent ventrally or united by a narrow glandular bar.

Etymology. *Conspectus*: conspicuous—a reference to the genital markings.

Distribution and habitat. Richmond Range; a specimen of *A. toonumbari* n.sp. was found in same sample.

Anisochaeta erica n.sp.

Fig. 10

Material examined. HOLOTYPE: AM W24448, (H), 500 m east of Junction Holes, near Barrington River, NSW, c. 31°59'S 151°45'E, 15.iii.1983, Ed Easton, "Jar 8 Sp 8" (mature, figured and dissected). (The sample also contained many specimens, AM W24536, that are possibly the smaller *A. palustris*, but are too immature to identify with certainty). PARATYPES: ANIC RB.98.2.15, (P1), Edwards Swamp, Barrington Tops, (?15).iii.1983, Ed Easton, "Jar 11 Sp 12", "c. 500 m West of Junction Pools—1 large specimen at depth of 2 ft" (mature, dissected); AM W24549, (P2), same details as H (juvenile with weak genital markings, dissected); AM W24450, (P3), same details as H (juvenile agrees superficially).

External features. Body mostly circular in section except tail which flares to form spade-shape. Lengths (mm): 100 (H), 120 (P1). Width: about 4 mm. Segments: 116 (H, P1), 96 (P2). Colour: uniform pale in alcohol. Prostomium: tapering epilobous; peristomium ventrally cleft. Clitellum: not developed but slightly marked in 14–17 in both H and P1. Dorsal pores: 3/4 minute, larger from 4/5. Setae: 24 on 12, 28 on 20, up to 32 on tail. Nephropores: not found. Spermathecal pores: small lateral pores in slight lips at anterior margin of segments 8 and 9 in *a* lines. Female pores: small paired on 14. Male pores: on 18 on small elliptical papillae approximately in *ab* lines. Genital markings: on 9–11 three sets of widely paired discs presetal and centred in *b* lines with tumid rim extending from *a* to *c* lines; in 18 and 19 two sets of paired white discs presetal in *b* lines, within common dark patch that surrounds both discs and male pores on each side (i.e., midventrum unmarked). This arrangement of genital markings pertains to H and P1.

Internal anatomy. Septa: 8/9–11/12/13 thickened. Gizzard: large muscular cone in 5 but displaced to occupy length of 7–9 and preceded by large crop. Oesophagus: four pairs of kidney-shaped calciferous glands in 11–14 attach laterally to oesophagus by short ducts; valvular in 15. Nephridia: avesiculate meroic, equatorial forests of numerous tubules,

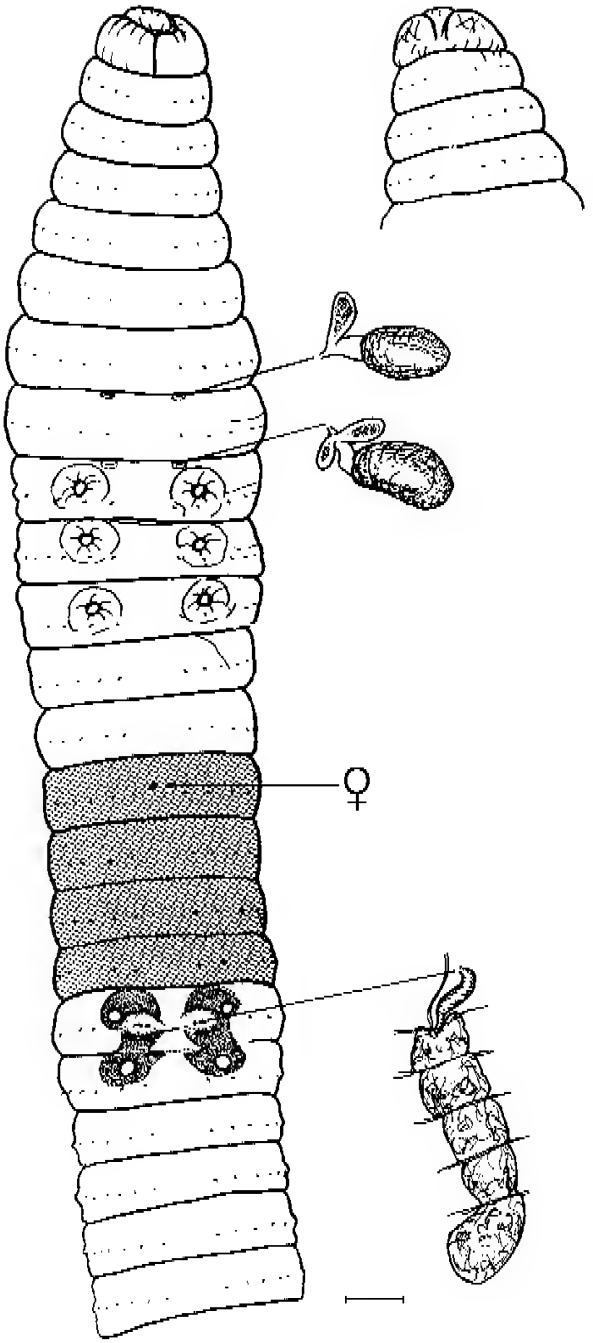

Figure 10. *Anisochaeta erica* ventral view of holotype with dorsal view of prostomium, spermathecae, and rhs prostate in 18–23 with vas deferens.

large in forebody, especially 6–9; smaller and fewer in intestinal segments where they number about eight per side; bladders and funnels not found. Vascularization: dorsal vessel single; hearts 10–12, supra-oesophageal vessel supplies calciferous glands. Spermathecae: two pairs in 7 and 8 but ducting to 7/8 and 8/9 (i.e., reflexed into preceding segments); conical ampulla on short duct joined ectally by short clavate diverticulum (8 rhs in H only has two diverticula). Male organs: holandric, small racemose seminal vesicles in 9 and 12; testes and funnels in 10 and 11. Ovaries: compact or elongate in 13; small paired ovisacs in 14. Prostates: elongate tubuloracemose in 18–23 (lhs in H deflected forwards 18–14); penial setae absent. Intestine: origin in 16 (septum 15/16 distended forwards); large T-shaped typhlosole develops from 16,17; gut contents brown organic loam.

Remarks. Four previously described *Anisochaeta* species from NSW are reported to have 4 pairs of calciferous gland. Fletcher's *A. monticola* has 4 pairs, but in segments 10–13, and, although similar with 2 pairs of spermathecae, differs in the distribution of genital markings, amongst other points. *Anisochaeta exigua* has 4 (or 5) pairs in 10–13,14, but has only one pair of spermathecae. *Anisochaeta macquariensis* has 3 (or 4) pairs in 10–13,14 but has 3 pairs of spermathecae. *Anisochaeta jenolanensis* has four pairs in 10–13, but has 4 pairs of spermathecae.

Anisochaeta erica is unique in having 3 pairs of calciferous glands in 11–14 and 2 pairs of spermathecae. Moreover, is has a distinctive arrangement of genital markings and a well-developed T-shaped typhlosole.

Etymology. *Erica*: heather—a reference to the habitat.

Distribution and habitat. Near Barrington River, Barrington Tops. From "area of heather-like shrubs" and from "tussock grass", the latter sample from depth of c. 60 cm. *Anisochaeta palustris* n.sp. is from the same area.

Anisochaeta filix n.sp.

Fig. 11

Material examined. HOLOTYPE: AM W24476, (H), Tree Fern Valley, New England National Park, NSW, c. 30°30'S 152°30'E, 17.iii.1983, Ed Easton, "Jar 15 Sp 31" (mature, figured and dissected). PARATYPES: ANIC RB.98.2.31, (P1), same details as H (mature, dissected); AM W24477, (P2), same details as H (mature); ANIC RB.98.2.32, (P3), same details as H (weakly clitellate mature); AM W24478, (P4), same details as H (mature); ANIC RB.98.2.36, (P5), same details as H (aclitellate mature, dissected).

External features. Body stout, circular in section except tail slightly spade-shaped. Lengths (mm): 135 (H), 150 (P1), 160 (P2), 125 (P3), 90 (P4), 110 (P5). Width: about 5–6 mm. Segments: 130 (H), 135 (P1). Colour: beige in alcohol with faint mid-dorsal line, clitellum puce, prostomium: tapering almost tanylobous; peristomium ventrally cleft. Clitellum: ½13 to ½17. Dorsal pores: 4/5 small dot, open from 5/6. Setae: 20 on 12, 24 on 20, about 32 on tail. Nephropores: not found. Spermathecal pores: wide openings in 7/8/9 in or just median to *b* lines. Female pores: paired on 14. Male pores: wide openings on 18 on apices of small round prominences approximately in *ab* lines, hollow trough between. Genital markings: on 9,10–11 and on 17 and 19, paired presetal sucker-like discs in *ab* (those in 9 absent in P1); smaller secondary pairs more median and postsetal on 11 (not in P4, P5), between male pores on 18 and single (or paired in P3) discs midventral on 19 (not in P5).

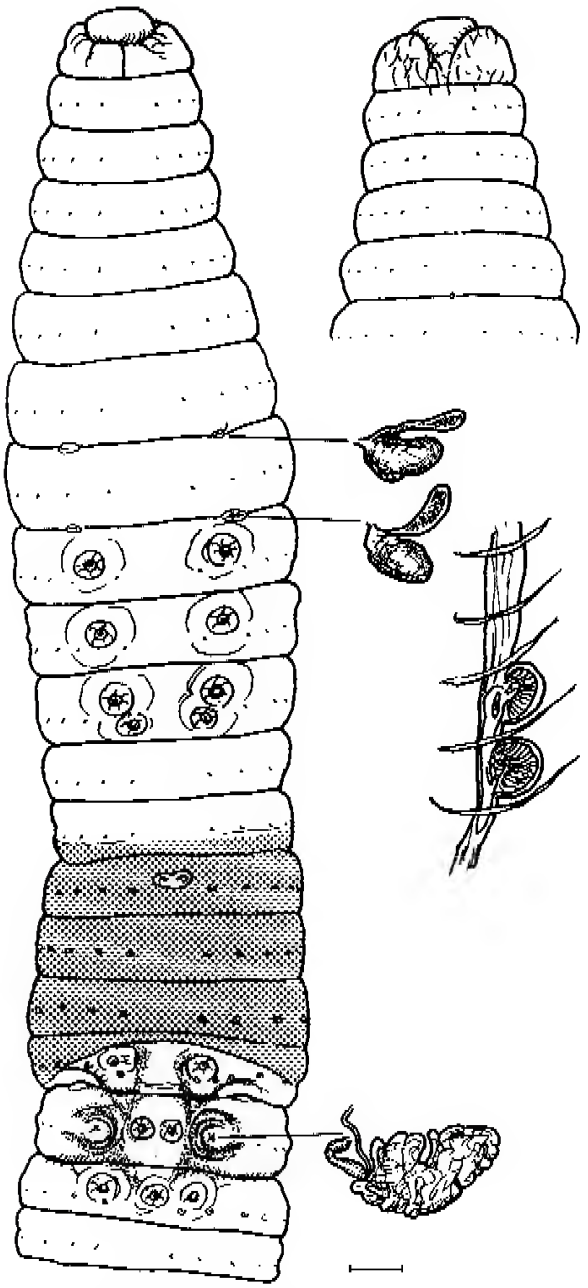

Figure 11. *Anisochaeta filix* ventral view of holotype with dorsal view of prostomium, spermathecae, oesophagus in 9–13 showing sectioned sessile calciferous glands on lhs in 11 and 12, and rhs prostate in 18 with vas deferens.

Internal anatomy. Septa: 7/8/9–12/13/14 slightly thickened. Gizzard: spheroidal muscular in 5. Oesophagus: in 11 and 12 two pairs of laterally sessile extramural calciferous glands; narrows in 14–15. Nephridia: avesiculate meroic, somewhat tufted in 5–6,7 then spread laterally as several equatorial, filamentous tubules; funnels and bladders not found. Vascularization: dorsal vessel single; hearts 10–12 from supra-oesophageal vessel which also branches to calciferous glands in 11 and 12. Spermathecae: two pairs in 8 and 9, tapering saccular ampulla poorly defined from duct with longer clavate diverticulum at base. Male organs: holandric, racemose seminal vesicles saccular in 9 and elongate in 12; testes and funnels in 10 and 11. Ovaries: palmate with numerous strings in 13; small paired ovisacs in 14. Prostates: flattened tubuloracemose in 18, duct short and overlain by tendons; penial setae absent. Intestine: origin in 16; true typhlosole absent; gut contents soil and fresh or decayed plant remains.

A slender, dark nematode was removed from the ventral blood vessel in P1 and sent to the Australian Museum nematologist, Dr G.L. Baker, for identification.

Remarks. *Anisochaeta filix* has two pairs of sessile calciferous glands in 11 and 12 and two pairs of spermathecae in 8 and 9. These characters are shared with *Anisochaeta macleayi* which is morphologically close. This latter species, recently redescribed in Blakemore & Elton (1994), differs in its less robust body, more lateral spermathecal pores and distribution of its genital markings. Especially distinctive in typical populations of *A. macleayi* are the two pairs of prominent mounds presetally in 10 and 11, each with an eye-like pore on its summit.

Etymology. *Filix*: fern—a reference to the locality name.

Distribution and habitat. Tree Fern Valley—from same sample as several other *Anisochaeta* spp (see *A. ancisa*).

Anisochaeta flava n.sp.

Fig. 12

Material examined. HOLOTYPE: AM W24543, (H), Washpool State Forest, NSW, c. 29°16'S 152°22'E, collected 9.iii.1992, M. Gray & P. Croft, pit trap sample set 22.ii.1992, "17CM Trap 2 FN 5081" (mature, figured and dissected). PARATYPES: ANIC RB.98.2.52, (P1), same location as H but "collected 22.ii.1992, set 6.ii.1992, Trap 2 FN5061" (mature, dissected); AM W24545, (P2), same details as P1 (mature, dissected); ANIC RB.98.2.53, (P3), same details as P1 (subadult); AM W24412, (P4), 200 m north of Twin Bridges, Gibraltar Range National Park, NSW, c. 29°30'S 152°20'E, c. 20.iii.1983, Ed Easton, "Jar 28 Sp 31" (mature, figured and dissected); ANIC RB.98.2.6, (P5), same details as P4 (mature, dissected).

Non-type material. AM W24413, (S1), same details as P4 (mature, dissected); ANIC RB.98.2.7, (S2), and AM W24414, (S3), same details as P4 (mature); ANIC RB.98.2.8, (S4), same details as P4 (mature, dissected); AM W24415, (S5–S11), same details as P4 (seven subadult or immature specimens).

External features. Body slightly dorsoventrally flattened. Lengths (mm): 88 (H), 90 (P1), 71 (P2), 62 (P4), 55 (P5). Width: about 3 mm. Segments: 86 (H), 126 (P1), 127 (P2), 110 (P4), 101 (P5). Colour: golden straw colour or uniform buff in alcohol, clitellum yellow, no mid-dorsal line. Prostomium: epilobous; peristomium ventrally cleft. Clitellum: ½13,14–16. Dorsal pores: from 4/5. Setae: 16 on 12, 16–18 on 20, about 20 on tail. Nephropores: not

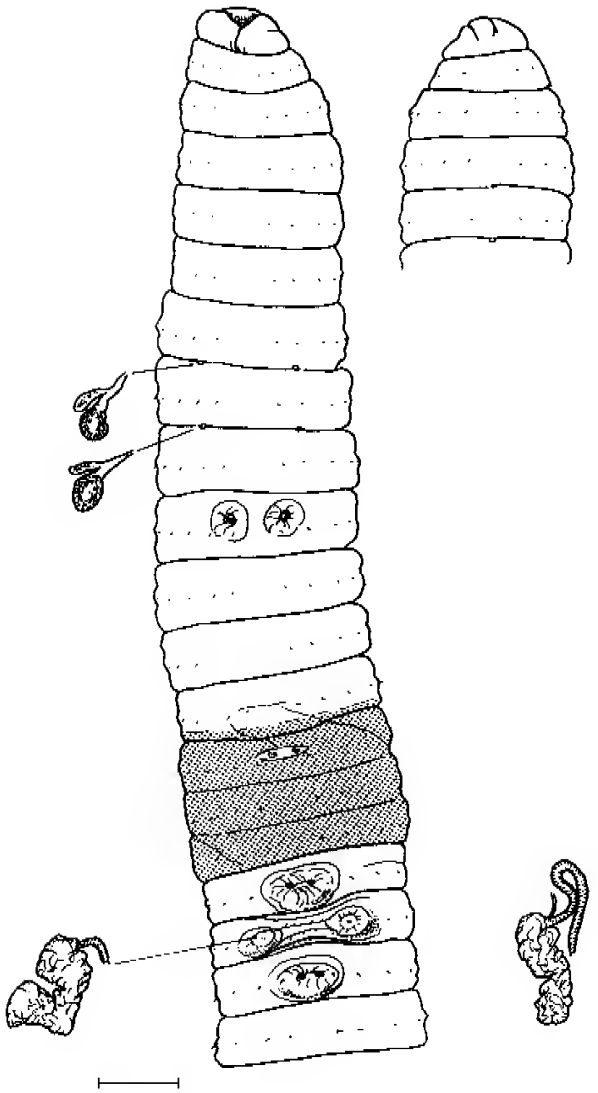

Figure 12. *Anisochaeta flava* ventral view of holotype with dorsal view of prostomium, spermathecae, and lhs prostate in 18–19 (prostate of P1 also figured with long duct and vas deferens).

found. Spermathecal pores: small in 7/8/9 in *ab* lines either closer to *b* or to *a* lines. Female pores: paired on 14. Male pores: on 18 on small round papillae approximately in *ab* lines and joined medially by small trough. Genital markings: on 10 paired sucker-like discs in *ab*, either presetal or postsetal; on each of 17 and 19, paired mid-ventral discs (sometimes discs linked by narrow line) near equator in common tumid pad that encompasses *aa*. Variations in genital markings: those in 10 are presetal in Washpool specimens, postsetal in Gibraltar specimens; in P5 the anterior markings are in 9 not 10; posterior markings are equatorial in Washpool specimens and elongate rather than paired in P2, but just postsetal in Gibraltar specimens, in P5 there is left-hand-side analogue only on 19.

Internal anatomy. Septa: none especially thickened (H) or slightly so in 8/9–11/12 (P4). Gizzard: large muscular in 5 but displaced to occupy length of 7–8. Oesophagus: increasingly dilated in 9–14 but not calciferous; narrowing in 15. Nephridia: avesiculate meroic, tufted in some or all of 4–6, then spread laterally with several small tubules per side. Vascularization: dorsal vessel single; hearts 10–12 connected to supra-oesophageal vessel. Spermathecae: two pairs in 8 and 9, spherical ampulla on slightly longer narrow duct with medium sized clavate diverticulum on duct (towards ental part in Washpool specimens, toward ectal end in Gibraltar specimens). Male organs: holandric, racemose seminal vesicles in 9 and 12; testes and funnels in 10 and 11. Ovaries: sheet-like in 13; small paired ovisacs in 14. Prostates: elongate tubuloracemose in 18–19, duct either short (H) or long, thin and folded back on itself (P1, P2, P4, P5); penial setae absent. Intestine: origin in 16; typhlosole absent; gut contents fine yellow or loamy soil.

Remarks. The distribution of genital markings distinguishes *A. flava* from other known species with two pairs of spermathecae and lacking calciferous glands. It compares with *A. noctiluca* (Jamieson & Wampler, 1979) from Lamington National Park, Queensland. In that species the genital markings differ being medianly conjoined presetal prominences on 10 with widely paired presetal pore-like centres plus unpaired glandular troughs on 17 and 19 that are, respectively, postsetal and presetal (i.e., not equatorial nor closely paired in 17 and 19 as in *A. flava*). Boardman's *Anisochaeta wiburdi* has markings in 9, 10, 17 and 19, but those in 9 are postsetal, those in 10 form a tetrad, and the paired equatorial pore-like markings in 17 and 19 are wider, immediately medial of setae *a* (see also *A. novaeanglica* n.sp.).

Varietal specimens, noted under non-type material above (S1–S11), resemble *A. noctiluca* by having puce pigmentation, 24 setae per segment in the forebody, spermathecae just lateral of *b* lines and markings in 17 and usually 19 that, while respectively postsetal and presetal, support paired discs like *A. flava*. As a consequence these are not attributed to *A. flava* nor *A. noctiluca* pending further investigation of permissible variation within these two taxa.

Etymology. *Flavus*: yellow, golden—a reference to the colouration.

Distribution and habitat. Washpool State Forest (with *Anisochaeta aemula, A. garilarsoni* and *A. lavatiolacuna*). Gibraltar range specimens were collected "in rainforest with tree fern" (with *A. calpetana*).

Anisochaeta garilarsoni n.sp.

Fig. 13

Material examined. HOLOTYPE: AM W24487, (H), Washpool State Forest, NSW, c. 29°16'S 152°22'E, collected 19.iii.1992, M. Gray & P. Croft, pit trap sample set 9.iii.1992, "17CM Trap 4 FN5093" (mature, figured and dissected). (H was damaged dorsally in 8–10 and a ?dipteran larva removed from the wound placed in a vial in the sample jar). PARATYPES: ANIC RB.98.2.50, (P1), same location as H but collected 9.iii.1992, set 22.ii.1992, "Trap 8 FN5087" (mature posterior amputee, dissected); AM W24541, (P2), same details as P1 but "Trap 2 FN5081" (mature,

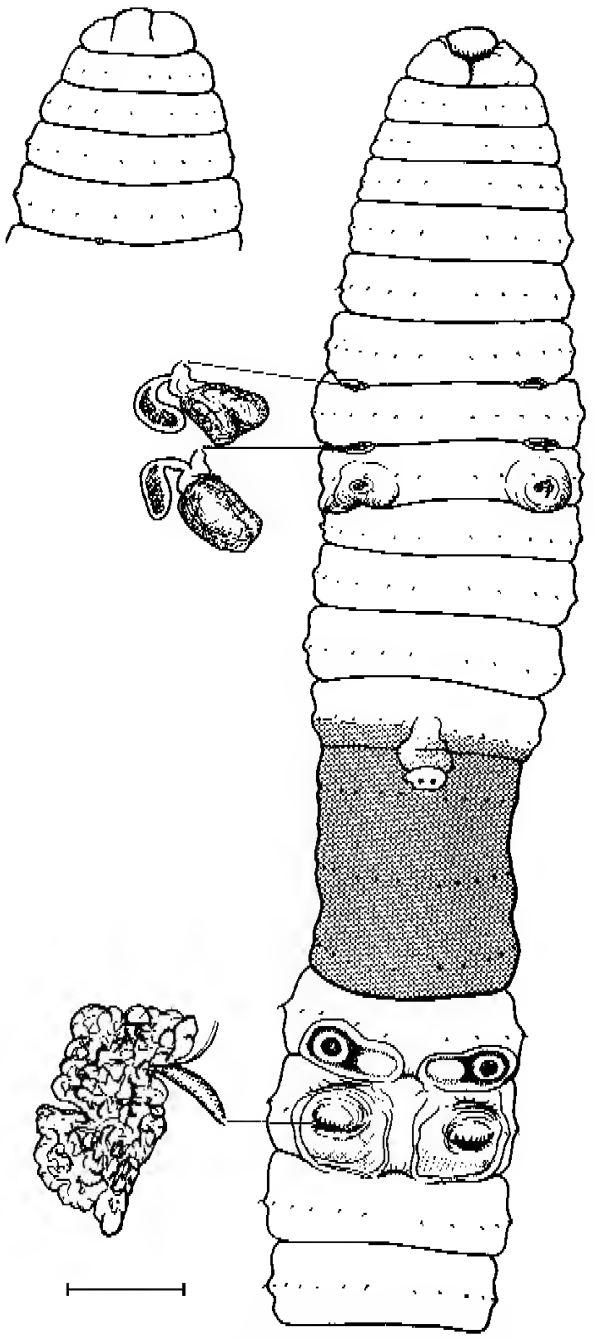

Figure 13. *Anisochaeta garilarsoni* ventral view of holotype with dorsal view of prostomium, spermathecae, and lhs prostate in 18–19 with vas deferens.

dissected); AM W24542, (P3, P4), same details as P2 (two specimens, a weakly clitellate mature, dissected, plus an immature that superficially agrees); ANIC RB.98.2.51, (P5), same details as P1 but "Trap 3, FN5082" (weakly clitellate mature); AM W24546 (P6), same details as P1 but collected 22.ii.1992 "Trap 2 FN5061" (aclitellate anterior amputee lacking first 4 segments).

Non-type material. AM W24570, (S1–S5), Twin Bridges, Gibraltar Range National Park, NSW, c. 29°30'S 152°20'E, 1,000 m, c. 20.iii.1983, Ed Easton, "Jar 27 Sp 31" (5 mature specimens which superficially agree, one exactly, the others have some variation of markings).

External features. Lengths (mm): range 42–60 mm, 60 (H), 46+ (P1), 58 (P2), 50 (P3), 42 (P5). Width: about 2 mm. Segments: 93 (H), 62+ (P1), 89 (P2). Colour: anterior dorsum dark red-grey, puce after clitellum fading to tail, clitellum buff. Prostomium: open epilobous; peristomium ventrally cleft. Clitellum: ½13,14–16 with dorsal dimple in 13. Dorsal pores: from 5/6. Setae: 24–28 per segment throughout. Nephropores: not found. Spermathecal pores: in 7/8/9 as widely paired lateral slits that occupy whole interval of *cd* or *de* lines. Female pores: paired on 14. Male pores: on 18 in wide and deep (eversible) pouches covered by thick hood approximately in *bc* lines, at centre of flat squarish rimmed pad that occupies ventral aspect of 18 from *a* to *c* lines on each side. Genital markings: large postsetal tumid mounds paired in *b-d* lines each with central pore in same line as spermathecae in 9 (H), or 10 (P2, P3, P5, P6) or lhs analogue only in 10 (P1); on 17 postsetally widely paired discs in *bc* lines with secondary less well defined pads more median and closer to posterior furrow, both markings within common rimmed pad on each side (all matures except P2 which lacks the outer discs on 17 but has additional pair midventrally in 18/19 in *aa*). Summary: markings usually paired postsetal in 9 or 10 and 17.

Internal anatomy. Septa: none especially thickened. Gizzard: compact weakly muscular in 5 (note: P2 is anomalous as gizzard is dislocated in segment 7). Oesophagus: only slightly dilated in 13–14, calciferous glands absent. Nephridia: avesiculate meroic, not especially tufted in anterior although tubules larger, spread laterally with about ten-twelve per side near anterior septa, reduced in size after clitellum; funnels and bladders not found. Vascularization: dorsal vessel single; hearts 10–12 from weak supra-oesophageal vessel. Spermathecae: two pairs in 8 and 9, saccular sometimes almost bifid ampulla on short duct with medium sized curving diverticulum at midlength. Male organs: holandric, thickly racemose seminal vesicles in 9 and 12; testes and funnels in 10 and 11. Ovaries: compact in 13; small paired ovisacs in 14. Prostates: flattened blocky tubuloracemose in 18–19,20, duct short; penial setae absent. Intestine: poorly differentiated from oesophagus, appears to be in 15 (in H) as dorsal blood vessel has lateral branches (cf. in 13–14) or 16 (in P1, P2, P3) as dorsal blood vessel is more closely applied (cf. more anteriorly); typhlosole absent; gut contents organic woody fragments and debris.

Remarks. With dark pigmentation and widely paired spermathecal pores, *Anisochaeta garilarsoni* is superficially similar to *A. aterpaenulata* and *A. virgata*, all three species also lack calciferous glands. However, *A. garilarsoni* is smaller, has fewer setae at least in the posterior, and lacks the genital markings on 19 that characterize these other two species. In other ways (e.g., shape of spermathecae, dorsal pores, intestinal origin), *A. garilarsoni* is somewhat intermediate to these two species although the hooded male pores are an additional distinction.

Etymology. Named in honour of Gary Larson, the cartoonist who has recently produced a popular booklet on earthworm ecology (Larson, 1998).

Distribution and habitat. Washpool State Forest (with *A. aemula, A. flava* and *A. lavatiolacuna*), and Gibraltar Range (with *A. bulla* varieties, *A. calpetana* and *A. flava*). Whether these pit trap specimens were damaged before or after capture, and the causes of the damage, are unclear.

Anisochaeta ima n.sp.

Fig. 14

Material examined. HOLOTYPE: AM W24576, (H), 100 m from base of Bald Rock, Bald Rock National Park, NSW, c. 28°51'S 152°03'E, 28.iii.1983, Ed Easton, "Jar 27 Sp 31" (mature, figured and dissected). PARATYPES: ANIC RB.98.2.63, (P1), same details as H (mature, dissected); AM W24577, (P2), same details as H (mature); ANIC RB.98.2.64, (P3), same details as H (mature); AM W24578, (P4–P16), same details as H (13 specimens: 2 mature, 8 aclitellate, 2 juveniles, some damaged).

External features. Body slightly dorsoventrally depressed and coiled. Lengths (mm): 70 (H), 90 (P1), 70 (P2), 85 (P3). Width: about 2–2.5 mm. Segments: 95 (H), 116 (P1). Colour: unpigmented in alcohol, clitellum pale. Prostomium: open epilobous with dorsal furrow; peristomium ventrally cleft. Clitellum: 14–16 but encroaches slightly onto adjacent segments. Dorsal pores: small in 3/4, open from 4/5 (occluded on clitellum). Setae: 20 throughout, but not all rows regular. Nephropores: not found but small pores seen at anterior of segments in line with every second or third seta in midbody. Spermathecal pores: 7/8/9 in *b* lines. Female pores: paired on 14. Male pores: on 18 in *ab* lines at centre of large flat pads that are darker and taper to mid-ventrum. Genital markings: in 11, tetrad of discs just lateral to and above and below setae *a* on each side, each disc within tumid pad that lies within *ab* lines, pads meet at setal arc to give overall 88 appearance (all mature specimens although sometimes one or two discs absent, one specimen has additional pair anteriorly on 10); on 17 paired oblique markings postsetal in *ab* lines (all specimens); on 19 small, paired pore-like dots just posteromedian to *a* setae within tumid pads that extend to *b* lines (all specimens except the one with markings in 10 where the dots are presetal).

Internal anatomy. Septa: 9/10–11/12 slightly thickened. Gizzard: large and muscular in 5 (and partly in 6 as septum 5/6 attaches at about mid-length). Oesophagus: dilated and vascularized but not calciferous, narrows in 15. Nephridia: avesiculate meroic, slightly tufted in 4–6 then as long stringy clusters of tubules that reduce in size after clitellum. Vascularization: dorsal vessel single; hearts 10–12 connected to weak supra-oesophageal vessel. Spermathecae: paired in 8 and 9, ampulla saccular on equally long duct with short, ectally bulbous diverticulum. Male organs: holandric, seminal vesicles racemose in 9 and 12, iridescent testes and funnels in 10 and 11. Ovaries: in 13 sheet-like with several egg strings, oocytes large; small ovisacs in 14. Prostates: tubuloracemose in 17–19, duct especially thick and muscular, penial setae absent. Intestine: from 16, deep lamellar typhlosole develops from 18, gut contents fine soil dark with charcoal.

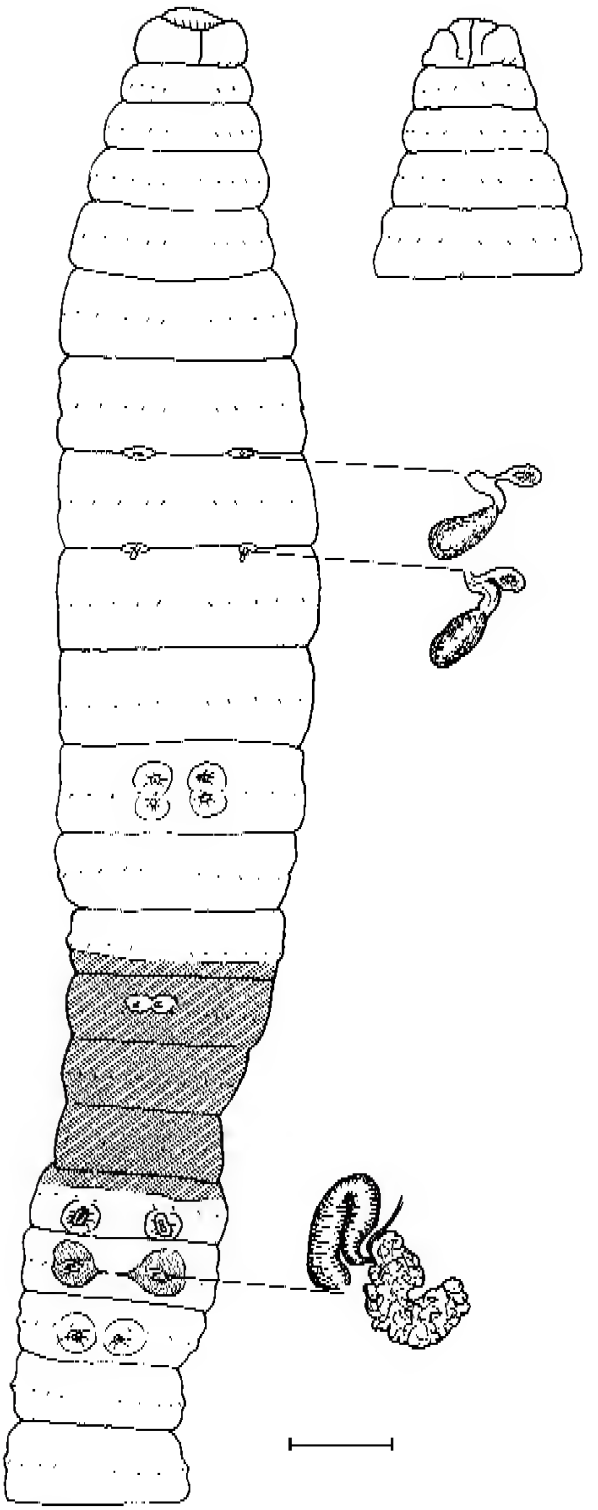

Figure 14. *Anisochaeta ima* ventral view of holotype with dorsal view of prostomium, spermathecae, and rhs prostate in 18–19 with thick duct looping into 17 and vas deferens.

Remarks. *Anisochaeta ima* typically has tetrad (88-like) markings on segment 11, similar markings are found in other congeneric species but usually they occur on segments 9 and 10 or 10 and 11 (i.e., most consistently on 10—see *A. novaeanglica*, this account). Such markings occur in *Anisochaeta tenax, Anisochaeta monticola* and *Anisochaeta jenolanensis*, being described as "8-shaped" or "8-like" by Fletcher. All three of these species occur in the vicinity of Sydney/Blue Mountain region and differ, at least, by having extramural calciferous glands. (In the current study, a sample of 4 specimens [AM W24493] from Blue Mountains were identified with *A. tenax*; having 88-like markings in 9 and 10, and three pairs of calciferous glands in 11–13. Slight differences from Fletcher [1886b: 953–955; 1890: 1014–1015] were that the dorsal blood vessel was not doubled and that the spermathecal diverticula were just longer than the ampullae).

Anisochaeta ima is further characterized by the distinctive male field, thick prostatic duct and the shape of the spermathecae.

Etymology. *Imus*: from the bottom or base of Bald Rock mountain.

Distribution and habitat. Bald Rock National Park, northeastern NSW, from soil under "ferns and eucalypts". *Anisochaeta aterpaenulata* and *A. calvasaxea* were collected nearby.

Anisochaeta lata n.sp.

Fig. 15

Material examined. HOLOTYPE: AM W24467, (H), Tree Fern Valley, New England National Park, NSW, c. 30°30'S 152°30'E, 17.iii.1983, Ed Easton, "Jar 15 Sp 31" (mature, dissected). PARATYPES: ANIC RB.98.2.24, (P1), same details as H (mature, slightly abnormal as segments 10–11, 11–12 fused ventrally, internal segmentation normal); AM W24468, (P2), same details as H (aclitellate mature, dissected); ANIC RB.98.2.29, (P3) same details as H (juvenile that agrees externally).

External features. Body circular in section with slightly spade-shaped tail. Lengths (mm): range 80–110 mm, 110 (H), 100 (P1), 80 (P2), 60 (P3). Width: about 3 mm. Segments: 110 (H, P2), 100 (P1). Colour: anterior dorsum grey-brown with darker mid-dorsal line, clitellum buff. Prostomium: open epilobous; peristomium ventrally cleft. Clitellum: ½13–16. Dorsal pores: from 5/6. Setae: 20 on 12, 22 on 20, about 40 on tail. Nephropores: not found. Spermathecal pores: in 6/7/8/9 in *cd* lines. Female pore: single on 14. Male pores: on 18 at centres of widely paired mounds that occupy *bc* at least, no setae intervene. Genital markings: on 19 paired discs just anterior and superior to *a* setae (all specimens).

Internal anatomy. Septa: 7/8–11/12 slightly thickened. Gizzard: compact muscular in 5, occupies one segment length. Oesophagus: increasingly dilated in 11–14, calciferous glands absent, valvular in 15. Nephridia: avesiculate meroic, clustered ventrally but not tufted in anterior, in midbody have ranks of about ten to twelve small tubules per side in two irregular rows near anterior septum and equatorial; funnels and bladders not found. Vascularization: dorsal vessel single onto pharyngeal mass in 4; hearts 10–12 from supra-oesophageal vessel traced 6–12. Spermathecae: three pairs in 7–9, spherical ampulla

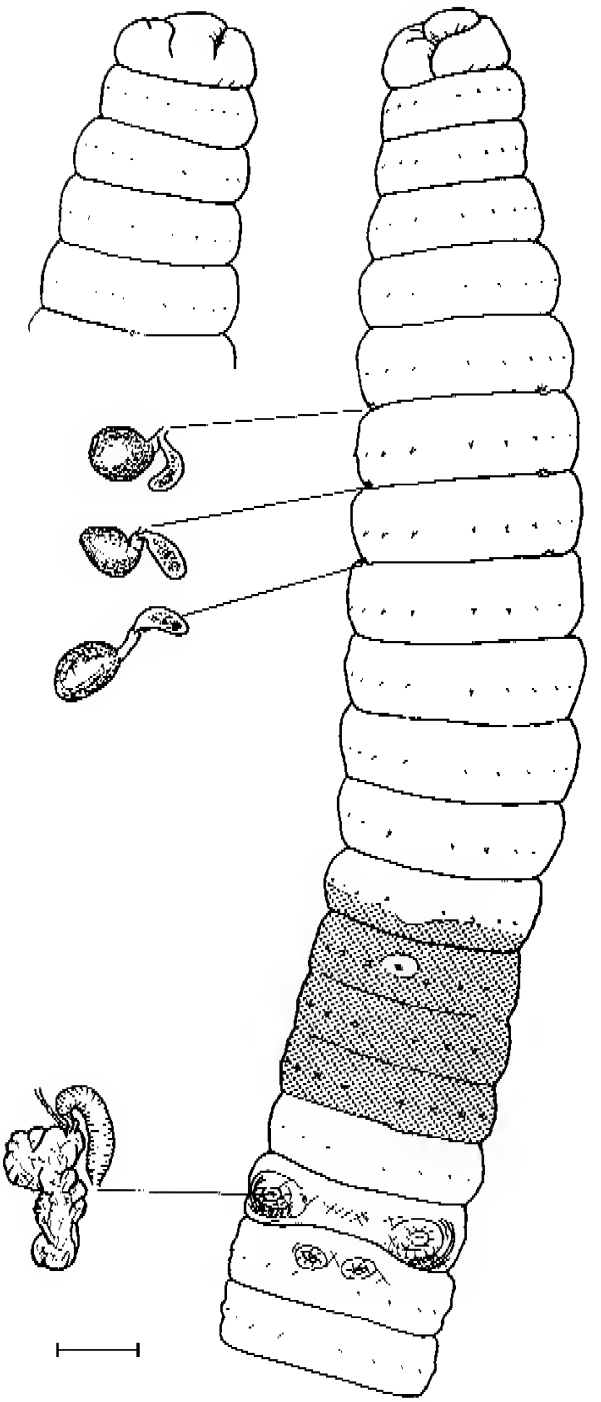

Figure 15. *Anisochaeta lata* ventral view of holotype with dorsal view of prostomium, spermathecae, and lhs prostate in 18–19 with thick looping duct and vas deferens.

on short duct with medium sized curving diverticulum ectally. Male organs: holandric, large seminal vesicles in 9 and 12; testes and funnels in 10 and 11. Ovaries: as long strings in 13; large paired ovisacs in 14. Prostates: blocky, tubuloracemose in 18–19, duct thick and curved; penial setae absent. Intestine: origin 16; typhlosole absent; gut contents colloidal soil with organic fragments.

Remarks. Having 3 pairs of spermathecae opening near *d* lines and lacking calciferous glands, *Anisochaeta lata* is similar to *A. gracilis* that differs with regards to the male field (described with male pores as transverse slits in *bc* lines, with seta *a* retained and a pair of papillae just anterior to the male pores; other genital markings are often wanting—see Fletcher, 1886b: 959 and Boardman, 1943, fig. 4). Moreover, *A. gracilis* has tufted nephridia, seminal vesicles in 11 and 12 and spermathecal diverticula that may be as long as the ampullae.

Characteristics of *A. lata* are three sets of widely paired spermathecal pores, lack of calciferous glands, genital markings in 19 and thick prostatic ducts (similar to those in *A. ima*).

Etymology. *Latus*: wide—a reference to the spermathecal and male pores.

Distribution and habitat. Tree Fern Valley, New England National Park.

Anisochaeta lavatiolacuna n.sp.

Fig. 16

Material examined. HOLOTYPE: AM W24485, (H), Washpool State Forest, NSW, c. 29°16'S 152°22'E, collected 19.iii.1992, M. Gray & P. Croft, pit trap sample set 9.iii.1992, "17CM Trap 4 FN5093" (mature, figured and dissected). (Specimen fragile, now broken in half). PARATYPES: ANIC RB.98.2.38, (P1), same details as H but "Trap 3 FN5092" (aclitellate mature, dissected); AM W24486, (P2), same details as P1 (juvenile, dissected).

External features. Lengths (mm): 44 (H), 30 (P1), 28 (P2). Width: about 1.5 mm. Segments: 88 (H), 98 (P1). Colour: pale unpigmented in alcohol, clitellum buff. Prostomium: open epilobous; peristomium ventrally cleft. Clitellum: ½13–16. Dorsal pores: from 5/6. Setae: 24 on 12 and on 20, about 30 on tail. Nephropores: difficult to determine, approximately lateral at anterior of segments in *g* or *h* lines. Spermathecal pores: in 4/5/6/7/8/9 in *cd* lines. Female pores: on 14, single (H, P2) or closely paired (P1). Male pores: on 18 on low mounds approximately in *bc* lines, no setae intervene. Genital markings: presetal discs in *bc* lines on 10 (paired H, P1, P2), on 11 (rhs only on H, paired P1, P2), on 12 (lhs only P1); postsetal discs on 19 large in *bc* lines just impinging on furrow 19/20 (H, P1, P2).

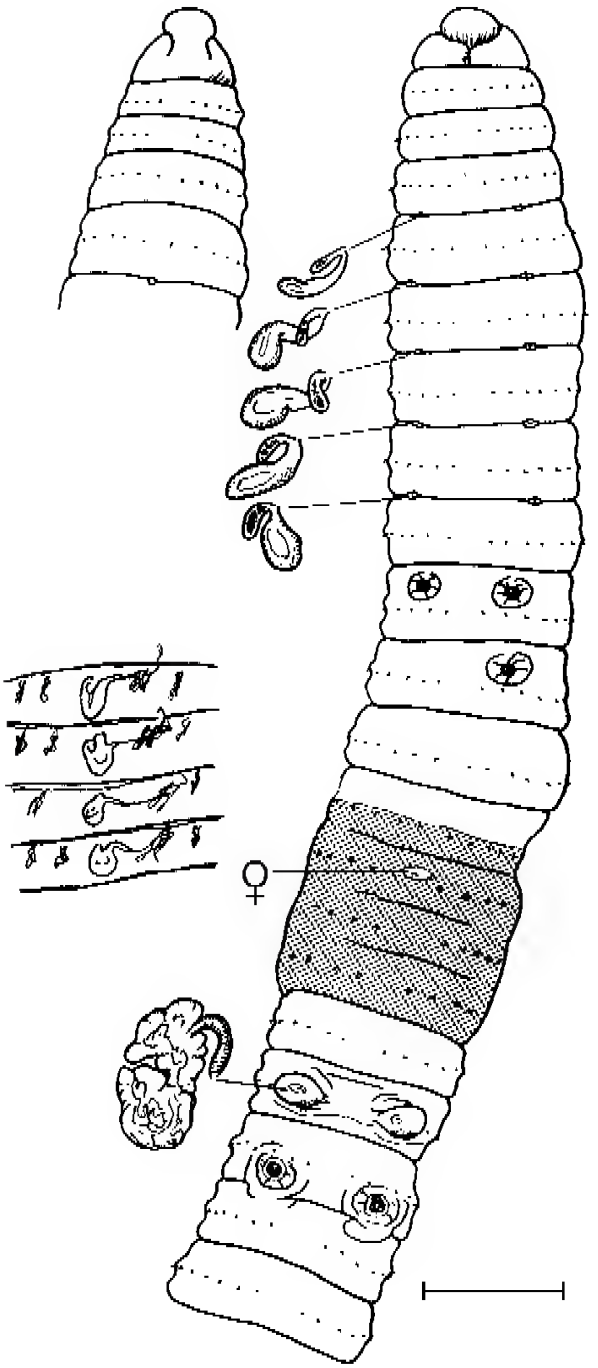

Figure 16. *Anisochaeta lavatiolacuna* ventral view of holotype with dorsal view of prostomium, spermathecae, nephridial arrangement on lhs around segments 23–26, and lhs prostate in 18–19.

Internal anatomy. Septa: none especially thickened. Gizzard: large but only slightly muscular in 5. Oesophagus: dilated in 13–14, calciferous glands absent, valvular in 15. Nephridia: vesiculate meroic, tufting not noted in anterior, about six per side, one lateral nephridium enlarged with preseptal funnel and V- or heart-shaped terminal bladder, other nephridia small and discrete near anterior septum. Vascularization: dorsal vessel single; hearts 10–12 from weak supra-oesophageal vessel in 7–12. Spermathecae: five

pairs in 5–9, conical ampulla on tapering duct with short diverticulum ectally. Male organs: holandric, seminal vesicles in 9 and, larger, in 12; testes and funnels in 10 and 11. Ovaries: as long strings in 13; small paired ovisacs in 14. Prostates: blocky tubuloracemose in 18–19, duct short curved; penial setae absent. Intestine: origin 16; typhlosole absent; gut contents yellow loamy soil.

Remarks. *Anisochaeta lavatiolacuna* has 5 pairs of spermathecae, lacks calciferous glands and has nephridial vesicles laterally. On this last character it resembles *A. aemula* and *A. toonumbari*, both of which, nevertheless, have only 2 pairs of spermathecae. Spencer (1893) describes *Anisochaeta* species from Victoria, several having 5 pairs of spermathecae, but all differ from *A. lavatiolacuna* at least with regards their genital markings.

Etymology. *Lavatio-lacuna*: wash-pool.

Distribution and habitat. Washpool State Forest (see *A. aemula, A. flava, A. garilarsoni*).

Anisochaeta liberalis n.sp.

Fig. 17

Material examined. HOLOTYPE: AM W24479, (H), Tree Fern Valley, New England National Park, NSW, c. 30°30'S 152°30'E, 17.iii.1983, Ed Easton, "Jar 15 Sp 31" (mature, figured and dissected). PARATYPES: ANIC RB.98.2.33, (P1), same details as H (mature, dissected); AM W24480, (P2), same details as H (mature); ANIC RB.98.2.34, (P3), same details as H (posterior amputee mature); AM W24481, (P4), same details as H (mature); ANIC RB.98.2.35, (P5), same details as H (posterior amputee mature); AM W24482, (P6) same details as H (posterior amputee mature).

External features. Lengths (mm): 150 (H), 165+ (P1), 130 (P2), 140 (P4). Width: about 5 mm. Segments: 115 (H), 122+ (P1), 123 (P2). Colour: uniform beige in alcohol (no mid-dorsal line), clitellum brick red. Prostomium: open epilobous; peristomium ventrally cleft. Clitellum: most of 13–17. Dorsal pores: small in 3/4, open from 4/5 (not on clitellum). Setae: 24 on 12, about 32 on 20, about 30 on tail. Nephropores: not found. Spermathecal pores: large within tumid lips in 7/8/9 in *b-c* lines. Female pores: on 14, paired or (P4) single. Male pores: on 18 on large opposed mounds approximately in *a-b,c* lines. Genital markings: irregularly outlined and asymmetrically paired mostly presetal papillae in *a-b,c* lines on 9 (often), 10 and 11 (always) and 12 (occasionally); two pairs of small discs near male porophores: one pair just anterolateral on 18, other pair posterolateral in 18/19; sunken arcs span both pairs of discs above and below the male porophores.

Internal anatomy. Septa: 9/10–12/13 with some thickening. Gizzard: large muscular cone in 5 but displaced to occupy 7–8, preceded by large crop. Oesophagus: not especially dilated (calciferous glands absent). Nephridia: avesiculate meroic, finely tufted in 5–6, then form parietal bands of numerous discrete tubules. Vascularization: dorsal vessel single; hearts 10–12 from supra-oesophageal vessel in 9–13. Spermathecae: two pairs in 8 and 9, saccular finely furrowed ampulla on tapering duct with medium sized diverticulum ectally. Male organs: holandric, seminal vesicles in 9 and 12; testes and funnels in 10 and 11. Ovaries: as delicate sheets in 13; small paired ovisacs in 14. Prostates: tubuloracemose in 18–20, duct narrow; penial setae absent. Intestine: origin 16 (deflects septum 15/16 anteriorly); deep T-shaped typhlosole develops from 19; gut contents fine colloidal soil and a few grits.

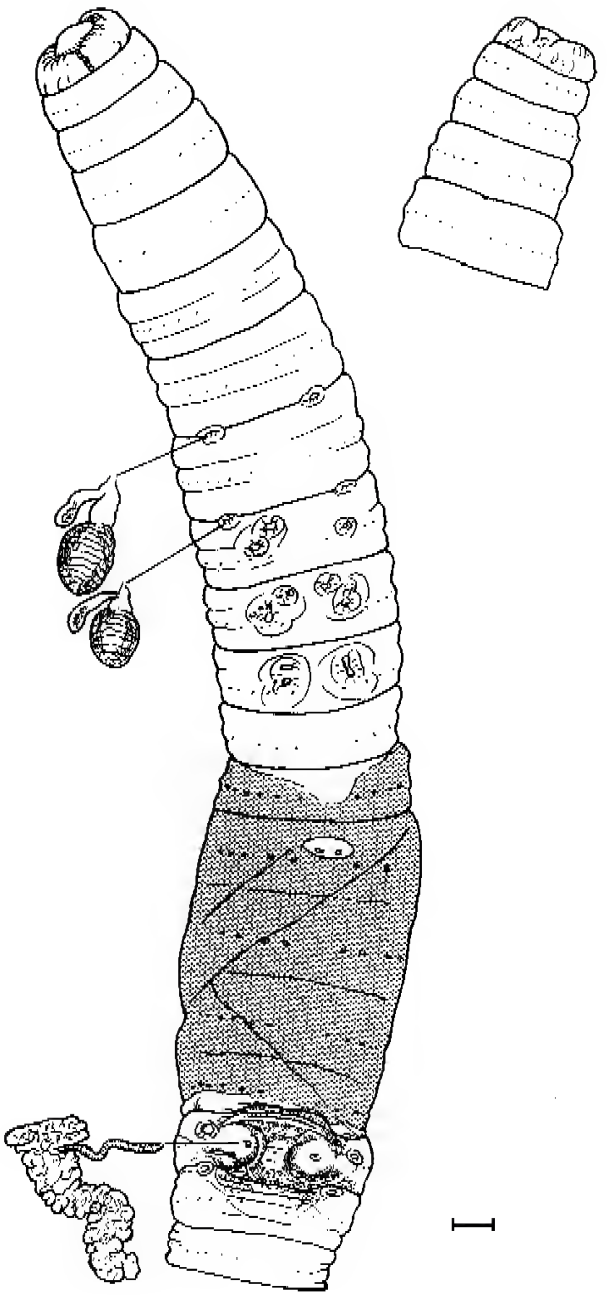

Figure 17. *Anisochaeta liberalis* ventral view of holotype with dorsal view of prostomium, spermathecae, and lhs prostate in 18–20.

Remarks. *Anisochaeta liberalis* compares with *A. rodwayi* that also has 2 pairs of spermathecae and lacks calciferous glands. Notable differences in the latter species are in the distribution of the genital markings—both more regularly paired and more ventral spots on 10, 11, 16, 17 and 19–21,22, the gizzard soft, and conspicuous dilations of the oesophagus in 10–13. Boardman (1943: 173–174) described specimens of *A. rodwayi* that have an additional pair of seminal vesicles in 10.

Distinctive characters of *A. liberalis* are the freely arranged genital markings in anterior segments (9–12), the opposed male porophores and the T-shaped typhlosole.

Etymology. *Liberalis*: handsome genital markings, freely or liberally distributed.

Distribution and habitat. Tree Fern Valley, New England National Park.

Anisochaeta novaeanglica n.sp.

Fig. 18

Material examined. HOLOTYPE: AM W24457, (H), Toms Cabin, New England National Park, NSW, c. 29°30'S 152°30'E, 18.iii.1983, Ed Easton, "Jar 17 Sp 8" (mature, figured and dissected). PARATYPES: ANIC RB.98.2.22, (P1), Tree Fern Valley, New England National Park, NSW, c. 30°30'S 152°30'E, 17.iii.1983, Ed Easton, "Jar 15 Sp 31" (mature, dissected); AM W24465, (P2), same details as P1 (mature, dissected); ANIC RB.98.2.23, (P3), same details as P1 (mature, dissected); AM W24469, (P4), same details as P1 (mature, posterior amputee); ANIC RB.98.2.28, (P5), same details as P1 (mature, complete).

External features. Lengths (mm): range 64–78; 64 (H), 78 (P1), 75 (P2), 65 (P3), 35+ (P4), 66 (P5). Width: 2.5–3 mm. Segments: range 95–114; 114 (H), 95 (P1), 105 (P2), 97 (P3). Colour: uniform buff in alcohol, clitellum light brown. Prostomium: open epilobous; peristomium ventrally cleft. Clitellum: 14–16 but encroaches slightly onto adjacent segments. Dorsal pores: small in 3/4, open from 4/5. Setae: about 24 throughout, tend to be less dense dorsally and not all rows regular. Nephropores: not found. Spermathecal pores: 7/8/9 in *b* lines. Female pores: paired on 14. Male pores: in 18 on slight mounds in *ab* lines. Genital markings: in 10 and 11, tetrads of discs just median to and above and below *a* setae within tumid pads that extend to setae *b* (all specimens); on 17 paired postsetal pads in *b-c* lines, conjoined by faint dark band (H, P1, P4) or dark patches only (P3, P5); small papillae sometimes present lateral to male pores (P1, P2, P3, P5); on 19 paired presetal dark patches below male pores (all specimens).

Internal anatomy. Septa: 10/11–12/13 slightly thickened. Gizzard: in 5 as large muscular barrel that occupies 7–9. Oesophagus: increasingly dilated in 9–13 with internal lamellae but not constituting calciferous glands, valvular in 15. Nephridia: avesiculate meroic, large in 5–7 but not tufted; equatorial bands of about twenty small tubules per side in midbody. Vascularization: dorsal vessel single; hearts 10–12 connected to weak supra-oesophageal vessel. Spermathecae: paired in 8 and 9, ampulla saccular on short duct with single diverticulum. Male organs: holandric, seminal vesicles racemose in 9 and 12, iridescent testes and funnels in 10 and 11. Ovaries: palmate in 13; ovisacs present in 14. Prostates: tubuloracemose in 18–20, penial setae absent. Intestine: from 16; deep lamellar typhlosole develops from 18 or 19; gut contents loamy soil.

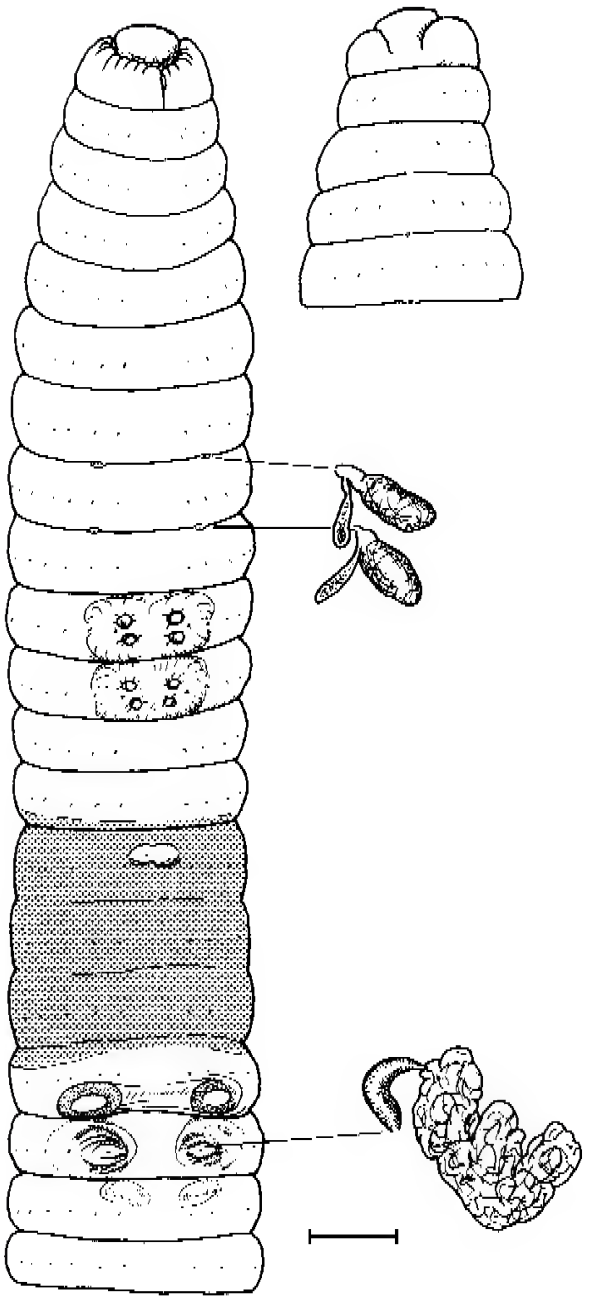

Figure 18. *Anisochaeta novaeanglica* ventral view of holotype with dorsal view of prostomium, spermathecae, and rhs prostate in 18–20.

Remarks. *Anisochaeta novaeanglica* is comparable with *A. curtisi* (Jamieson & Wampler, 1979) from Blackall Range and Lamington Plateau, southeastern Queensland, that was placed in a *cormieri* species-group characterized by absence

of calciferous glands (Jamieson & Wampler, 1979: 640). *Anisochaeta curtisi* was differentiated from the only other member of this group then known to have a tetrad of pore-like markings in 10 (that is *A. wiburdi*), by its having these far median to setae *a* (Jamieson & Wampler, 1979: 647). *Anisochaeta novaeanglica*, then, is differentiated from *A. curtisi* by having these markings wider, just median to setae *a*, and from *A. wiburdi* by having these markings narrower than *ab* lines (see also *A. ima*). *Anisochaeta novaeanglica* further differs from both these species by having lighter pigmentation (although preservation may cause bleaching), diverticula which do not extend distally as far as the ampullae, and the presence of a typhlosole. The importance of this latter character is uncertain as a typhlosole may be present or absent in varieties of some species (e.g., *A. bulla*).

Etymology. *Novae-anglica*: of New England.

Distribution and habitat. New England National Park, northeastern NSW, found in association with several other congeneric species.

Anisochaeta palustris n.sp.

Fig. 19

Material examined. HOLOTYPE: AM W24451, (H), Edwards Swamp, c. 500 m west of Junction Pools [sic], north bank of Barrington River, NSW, c. 31°59'S 151°45'E, ?15.iii.1983, Ed Easton, "Jar 11 Sp 31" (mature, figured and dissected). PARATYPES: ANIC RB.98.2.16, (P1), same details as H (mature, dissected); AM W24552, (P2), same details as H (weakly clitellate mature, dissected); ANIC RB.98.2.17, (P3) same details as H (weakly clitellate mature, dissected); (original sample contained several immature specimens that possibly belong to several species). AM W24453, (P5–P8), 200 m east of Junction Holes, 5 m above Barrington River, NSW, c. 31°59'S 151°45'E, 15.iii.1983, Ed Easton, "Jar 7 Sp 8" (five specimens that superficially agree, 4 matures, one clitellate, three aclitellate, one damaged, and one immature).

External features. Body circular in section. Lengths (mm): 55 (H), 50 (P1), 40 (P2, P3). Width: 1–2 mm. Segments: 90 (H), 98 (P1). Colour: pale unpigmented in alcohol, clitellum orange. Prostomium: closed epilobous; peristomium ventrally cleft. Clitellum: ½13 to ½17. Dorsal pores: small dot in 3/4, open from 4/5. Setae: 16 on 12, 16–18 on 20, 16–20 on tail. Nephropores: not found. Spermathecal pores: within tumid lips in 7/8/9 in *ab* but closer to *a* lines. Female pore: single on 14. Male pores: on 18 near setal *a* lines on slight mounds within sunken field that extends from setal arcs of 17 and 19 as wide as *b* lines. Genital markings: in 10 and 11, paired presetal discs in *ab* lines, (in H with small ancillary disc median and just superior to those in 10); small papillae at edges of male field in 17/18 and 18/19, single mid-ventral in 17/18 and closely paired mid-ventral in 18/19 (in all specimens except P2, P3 which have only preclitellar markings).

Internal anatomy. Septa: none especially thickened. Gizzard: in 5, small muscular, elongate and not much wider than pharynx. Oesophagus: narrow except for 13 and 14 which are dilated with internal lamellae (= two annular

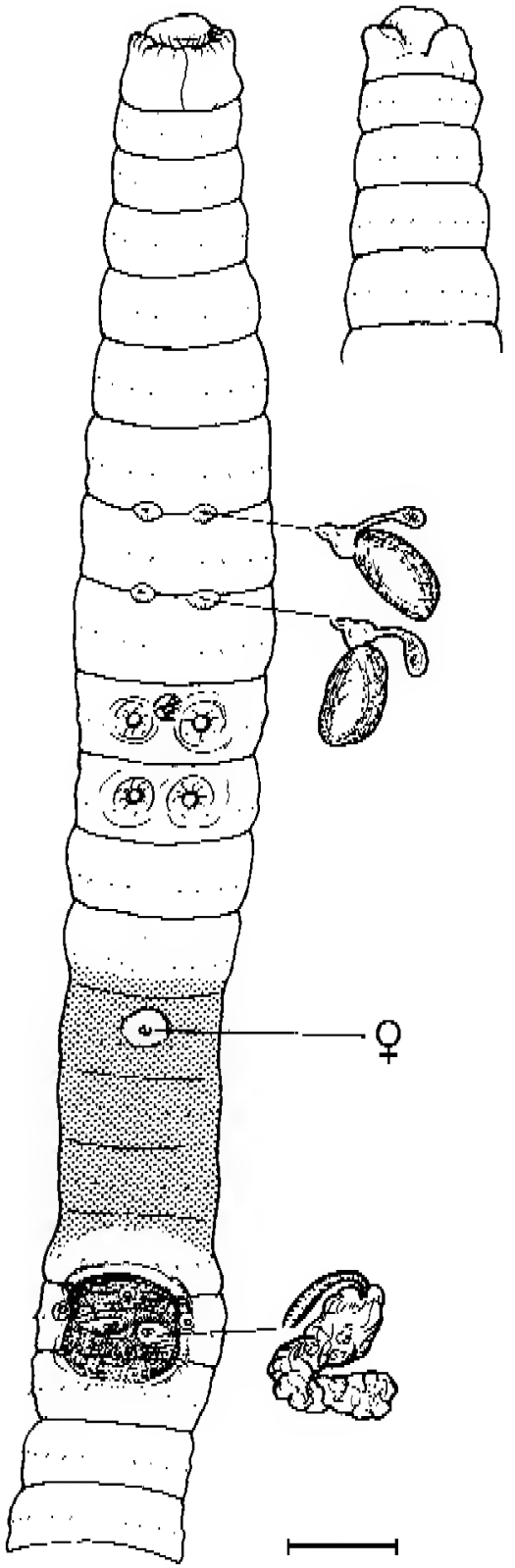

Figure 19. *Anisochaeta palustris* ventral view of holotype with dorsal view of prostomium, spermathecae, and rhs prostate in 18–19.

calciferous glands); narrow in 15 to ½16 (= valve). Nephridia: avesiculate meroic, equatorial bands of numerous tubules, large in 5–8 but not definitely tufted, smaller in midbody. Vascularization: dorsal vessel single onto pharyngeal mass in 4; hearts large in 10–12. Spermathecae: paired in 8 and 9, turgid orange ampulla saccular on short duct which is dilated midlength where joined by single medium sized diverticulum. Male organs: holandric, seminal vesicles in 9 and 12, iridescent testes and funnels in 10 and 11. Ovaries: palmate with numerous strings in 13; ovisacs paired in 14. Prostates: tubuloracemose in 18–19, penial setae absent. Intestine: from ½16; typhlosole absent; gut contents woody organic debris.

Remarks. *Anisochaeta palustris* has 2 pairs of spermathecae in *ab* lines and lacks extramural calciferous glands although the oesophagus has annular glands in 13 and 14 (cf. those in 11 and 12 in *A. filix*). It is unique in the arrangement of genital markings: large paired discs presetal in 10, 11 and insunk male field often with regularly arranged small papillae. The large spermathecal pores and preclitellar genital markings are reminiscent of those in *A. ancisa*, and *A. conspecta* which are also morphologically similar. However, these two species have a few more setae, larger gizzards, and differ in their respective arrangements of posterior genital markings, as well as lacking the annular oesophageal glands in 13 and 14.

AM W24536, consisting of several specimens from 500 m east of Junction Holes, Barrington River, NSW, c. 31°59'S 151°45'E, 15.iii.1983, Ed Easton, "Jar 8 Sp 8", resemble *A. palustris* superficially but the one dissected had five pairs of extramural calciferous glands in 10–14 so is not conspecific.

Etymology. *Palustris*: from the swamp.

Distribution and habitat. Edwards Swamp, Barrington River, from tussock grass.

Anisochaeta paucula n.sp.

Fig. 20

Material examined. HOLOTYPE: AM W24484, (H), Tree Fern Valley, New England National Park, NSW, c. 30°30'S 152°30'E, 17.iii.1983, Ed Easton, "Jar 15 Sp 31" (mature, figured and dissected). PARATYPES: ANIC RB.98.2.37, (P), same details as H (mature, dissected).

External features. Lengths (mm): 38 (H), 30 (P). Width: about 1.5 mm. Segments: 83 (H), 90 (P). Colour: straw coloured in alcohol; clitellum buff. Prostomium: tapering epilobous; peristomium ventrally cleft. Clitellum: ½13 to ½17. Dorsal pores: from 5/6. Setae: about 14 on 12 and on 20, 18 on tail. Nephropores: not found. Spermathecal pores: in 7/8/9 in or near *b* lines. Female pores: paired on 14. Male pores: small on 18 at centres of small circles in ab. Genital markings: (H, P) small paired presetal discs on 10 in *ab*, on 19 centred in *a* and on 20 just median of *a* lines.

Internal anatomy. Septa: 7/8–12/13 slightly thickened. Gizzard: in 5, muscular compact. Oesophagus: not modified,

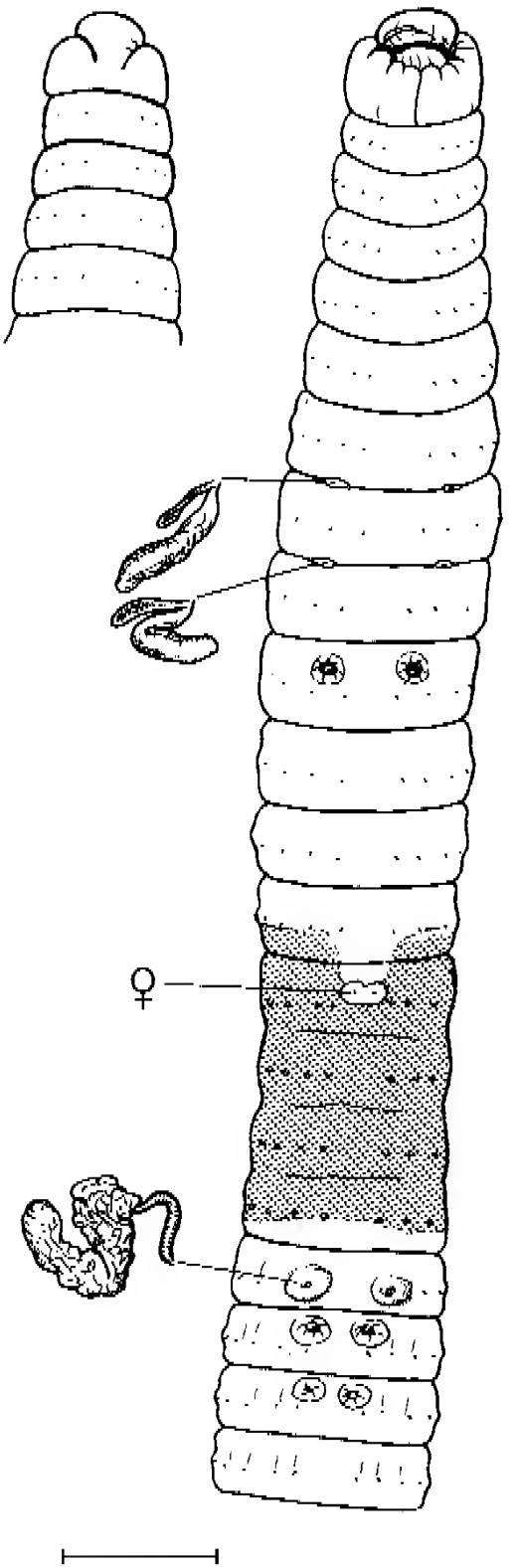

Figure 20. *Anisochaeta paucula* ventral view of holotype with dorsal view of prostomium, spermathecae, and rhs prostate in 18.

valvular in 15 and part of 16. Nephridia: avesiculate meroic, tufts not demonstrable, in anterior two sets of tubules per side (seen in segments 8 and 13), in intestinal segments three sets of tubules per side; bladders and funnels not found. Vascularization: dorsal vessel single; large hearts in 10–12 from weak supra-oesophageal vessel in 9–12. Spermathecae: 8 and 9, elongate ampulla tapers to duct with medium length clavate diverticulum near base. Male organs: holandric, seminal vesicles in 9 and 12, iridescent testes and funnels free in 10 and 11. Ovaries: long palmate in 13; small ovisacs in 14. Prostates: tubuloracemose in 18 on narrow duct, penial setae absent. Intestine: origin ½16,16; typhlosole absent; gut contents organic soil.

Remarks. *Anisochaeta paucula* is distinguished from morphologically similar species described in this paper by its small size, few setae, reduced numbers of nephridia and the distribution of its small genital markings in 10, 19 and 20.

Etymology. *Pauculus*: very few—for the reduced nephridia.

Distribution and habitat. Tree Fern Valley, New England National Park.

Anisochaeta rava n.sp.

Fig. 21

Material examined. HOLOTYPE: ANIC RB.97.5.4, (H), Bago-Maragle State Forests, NSW; Ecologically Sustainable Management Project Sample BM110, location details are given as "off De Beazevilles Rd; bearing point is 210 m E of Poison Rock Ck crossing on hillcrest—then bearing 186° for 40 m", Courabyra Sheet No. 8526-4S DGPS AMG 611318 6056240; elevation 1,115 m; shallow basalt soil with high worm activity; P.J. Ryan, 24.iv.1996, (mature, figured and dissected). PARATYPES: none.

External features. Length 75 mm. Width: 3.5–4.0 mm. Segments: 135. Colour: uniform grey in alcohol. Prostomium: tapering epilobous; peristomium ventrally cleft. Clitellum: 14 to ½17. Dorsal pores: small in 3/4, wider from 4/5. Setae: 20 on 12 and 20, about 28–30 on tail. Nephropores: not found. Spermathecal pores: in 6/7/8/9 in mid-*ab* lines. Female pores: paired on 14. Male pores: small in *ab* lines within common dumb-bell shape. Genital markings: on 9 and 10, small postsetal discs in *bc* lines, those on 10 combined with additional presetal pair (to give a wide tetrad of 88-like markings); on 16, 17 and 19, 20 mid-ventral tumid pads equatorial extending to *b* lines, some with weakly defined pore-like discs median of *a* lines.

Internal anatomy. Septa: none especially thickened. Gizzard: large in 5, muscular aubergine-shaped displaced to occupy most of length of segment 6–8. Oesophagus: dilated and white in 11–12, but calciferous glands absent. Nephridia: avesiculate meroic, tufted in 4 and 5, then reduce in size to become equatorial bands of numerous tubules; bladders and funnels not found. Vascularization: dorsal vessel single onto pharyngeal mass; hearts in 10–12. Spermathecae: three pairs in 7–9, ampulla elongate tapering to duct with long clavate diverticulum near base. Male organs: holandric, seminal vesicles in 9 and 12, iridescent testes and funnels free in 10 and 11. Ovaries: palmate in 13; ovisacs not found. Prostates: bilobed racemose in 18–19, penial setae absent. Intestine: origin ½16; deep lamellar typhlosole develops from 19; gut contents reddish soil.

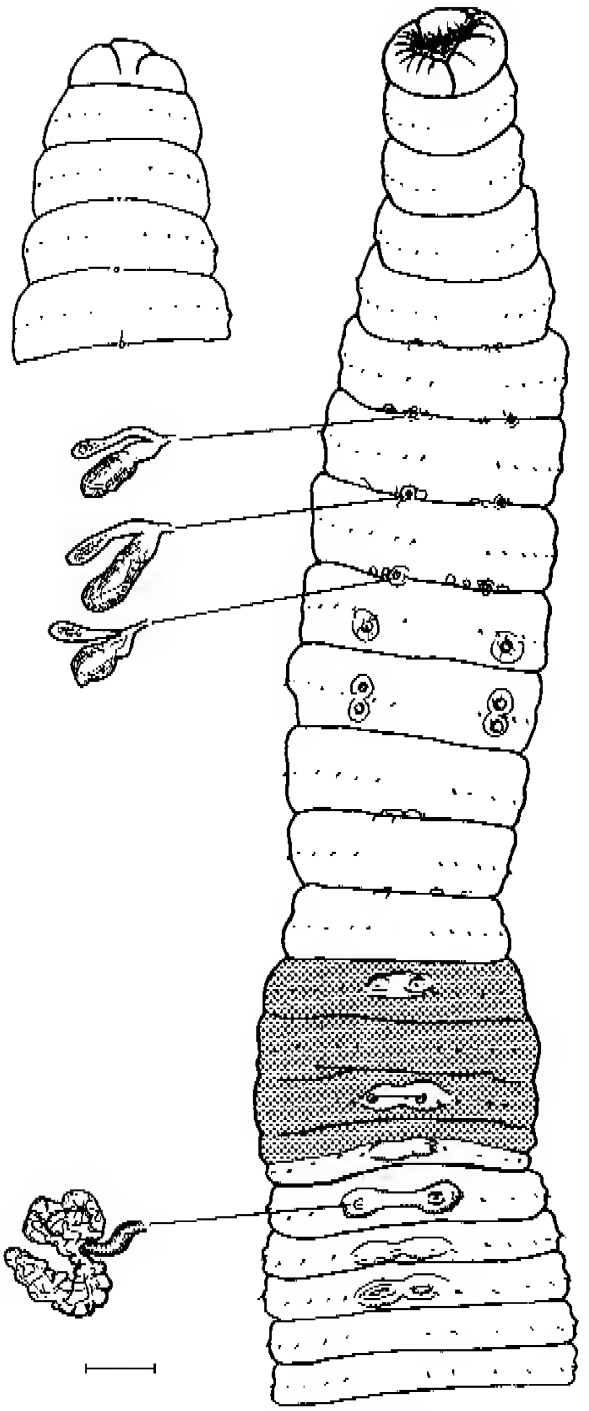

Figure 21. *Anisochaeta rava* ventral view of holotype with dorsal view of prostomium, spermathecae, and lhs prostate in 18–19.

Remarks. *Anisochaeta rava*, with three pairs of spermathecae in *ab* lines and lacking calciferous glands, is morphologically similar to *A. celmisiae*. They are primarily distinguished

by differences in the distributions of genital markings. Markings in *A. celmisiae* are typically paired low prominences on 10 each with central pore-like disc presetal and median to *b* (sometimes extra postsetal disc present to form tetrad on 10 but still median to *b* lines rather than lateral as in *A. rava*); smooth midventral markings mostly postsetal in 17, and mostly presetal in 19; plus markings, pore-like or ridges, lateral to male pores. *Anisochaeta rava* has discs on 9 and 10, mid ventral pads on 17 and 19 and lacks markings on 18. Additionally, *A. rava* has a stronger gizzard and a typhlosole.

Etymology. *Ravus*: grey.

Distribution and habitat. Bago-Maragle State Forests are adjacent to and west of Kosciuszko National Park. These specimens were collected as part of a multi-disciplinary survey of forest soil ecosystem conducted by CSIRO, the Australian National University, and various state Forestry Departments. All fauna collections were made by Phil Ryan and Neil McKenzie (CSIRO Forestry, Canberra), and David Jacquier and Peter Leppert (CSIRO Land and Water). Further site and soil survey details can be obtained from Dr Phil Ryan. Found at the same general locality was *A. rubeospina.*

Anisochaeta rubeospina n.sp.

Fig. 22

Material examined. HOLOTYPE: ANIC RB.97.5.5, (H), Bago-Maragle State Forest; NSW, ESM Sample BM126; "2° and 250 m from track/crest", Courabyra Sheet No. 8526-4S DGPS AMG 603014 6052807; elevation 1,295 m; granodiorite soil; N.J. McKenzie, 23.v.1996, (mature, figured and dissected). PARATYPES: AM W25447, (P1), same details as H, (mature, dissected); ANIC RB.97.5.7, (P2), same details as H, (mature, dissected).

External features. Lengths (mm): 80 (H), 75 (P1), 100 (P2). Width: 4.5–5.0 mm. Segments: 132 (H), 104 (P1). Colour: anterior dorsum dark brown with distinct darker red mid-dorsal line continued to tail, otherwise pale; clitellum buff. Prostomium: tapering epilobous; peristomium ventrally cleft. Clitellum: ½13 to ½17,17. Dorsal pores: small in 3/4, wider from 4/5. Setae: about 20 on 12, about 24 on 20 and on tail. Nephropores: not found. Spermathecal pores: small in 6/7/8/9 in *a* lines. Female pores: paired on 14. Male pores: on opposed prominences in *a* lines. Genital markings: on 10 paired squarish pads, conjoined anteriorly, extending *a-c* lines with lateral slits presetally in *a-b*; midventral elliptical pads with central slit-like depressions in *aa* in 16, 17 19, in *bb* in 20, 21; paired tumid discs lateral to male porophores, one pair superior, one pair inferior, tumid between on either side. Variations in marking are: on P1 on 10 eye-like and on 18 only one pair of papillae immediately lateral to male porophores, otherwise same; P2 has no markings on 10, and longitudinal ridges without papillae lateral to male pores, otherwise same.

Internal anatomy. Septa: 8/9–12/13 slightly thickened. Gizzard: in 5, large muscular barrel with anterior flange. Oesophagus: in 10–12, three pairs of lateral calciferous pouches, each with internal lamellae. Nephridia: avesiculate meroic, tufted in 4 and 5, then reduce in size to become

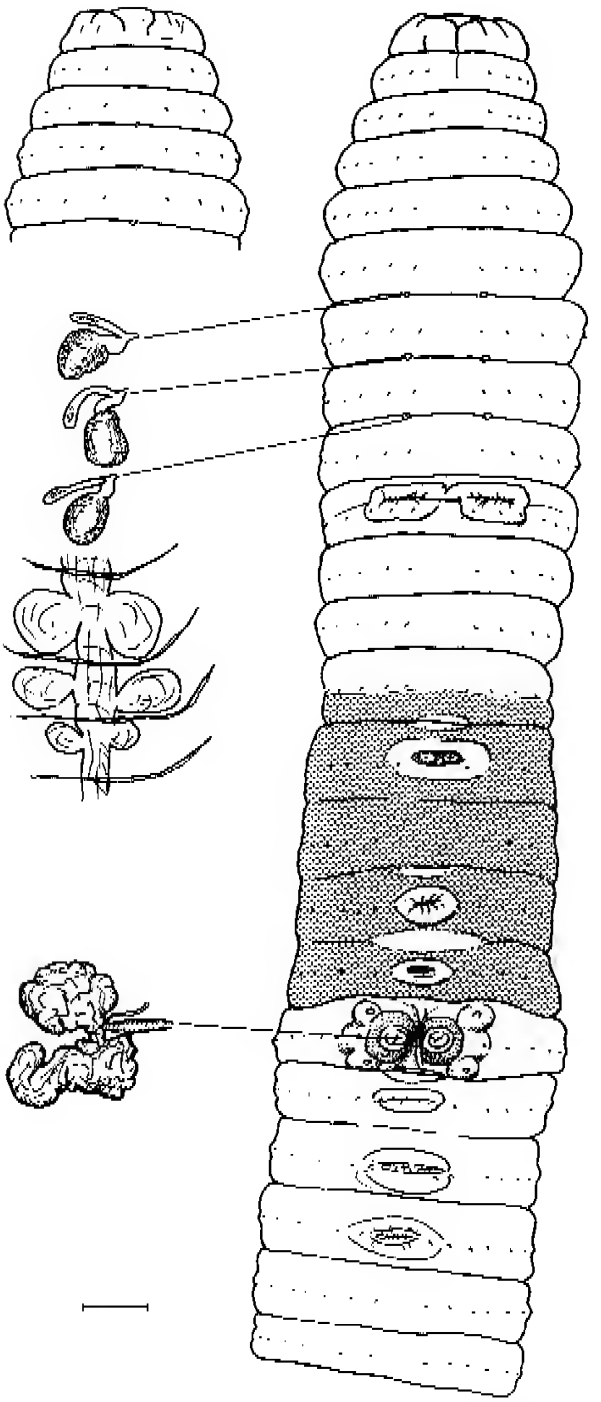

Figure 22. *Anisochaeta rubeospina* ventral view of holotype with dorsal view of prostomium, spermathecae, calciferous pouches on the oesophagus in 10–12, and lhs prostate in 18–19 with vas deferens.

equatorial bands of numerous tubules, ten or more per side; bladders and funnels not found. Vascularization: dorsal vessel single onto pharyngeal mass; hearts in 10–12 from supra-oesophageal vessel. Spermathecae: three pairs in 7–9, saccular ampulla on narrow duct with medium length clavate diverticulum near base. Male organs: holandric, seminal vesicles in 9 and 12, testes and funnels in mucus in

10 and 11. Ovaries: small in 13; ovisacs not found. Prostates: bilobed racemose in 18–19, penial setae absent. Intestine: origin 15; typhlosole absent; gut contents organic debris and woody material.

Remarks. *Anisochaeta rubeospina* has 3 pairs of spermathecae and 3 pairs of pouch-like calciferous glands. Known species with this arrangement (*A. austrina, A. raymondiana, A. chani* and *A. hamiltoni*) all differ by having spermathecal pores in *b* lines and intestinal origin in 16 and in the distributions of their genital markings.

Etymology. *Rubeo-spina*: red spine.

Distribution and habitat. Bago-Maragle Forest, same survey project and locality as *A. rava*, but site details not available.

Anisochaeta toonumbari n.sp.

Fig. 23

Material examined. HOLOTYPE: AM W24488, (H), Toonumbar State Forest, NSW, 28°28'S 152°43'E, 27.iii.1983, Ed Easton, "Jar 34 Sp 50" (mature, figured and dissected). PARATYPES: ANIC RB.98.2.39, (P1), same details as H (mature, dissected); AM W24489, (P2), same details as H, (mature posterior amputee, dissected); ANIC RB.98.2.40, same details as H, (mature posterior amputee); AM W24490 (P4), same details as H, (mature); ANIC RB.98.2.41 (P5), same details as H, (aclitellate mature); AM W24491, (P6), same details as H, (weakly clitellate mature); ANIC RB.98.2.42, (P7), same details as H, (mature); AM W24492, (P8–P14), same details as H, (7 specimens, one an anterior portion of a mature, six aclitellate matures plus 7 tail fragments in original sample jar). AM W24562, (P15), Richmond Range State Forest, NSW, 28°31'S 152°44'E, c. 27.iii.1983, Ed Easton, "Jar 35 Sp 31" (aclitellate mature, dissected).

External features. Pharynx everted in H. Lengths (mm): range 60–80; 80 (H), 60 (P1), 66 (P4), 80 (P6), 65 (P7), 70 (P15). Width: about 2–3 mm. Segments: 123 (H), 100 (P1). Colour: unpigmented (bleached) in alcohol; clitellum reddish. Prostomium: epilobous (P1 and other specimens); ventral cleft weak or absent. Clitellum: ½13–16 (H and P1, P2) or ½13,14 to ½16 (in P3, P4, P7). Dorsal pores: 3/4 small, open from 4/5. Setae: small and difficult to count, about 20 throughout most of body with 20–16 counted on tail. Nephropores: not found. Spermathecal pores: in 7/8/9 small pores within large lips in *b* lines. Female pores: closely paired on 14. Male pores: on tips of small eversible penes in *ab* lines on small elliptical porophores, no setae intervene. Genital markings: (in H only) on 10 and 11 large midventral sucker-like discs with tumid borders extending to *a* or *b* lines; segments 16 and 17 (postsetally), and 18 (presetally) each with two pairs of laterally conjoined discs, the outer pair large and circular in approximate line of male pores, the inner pair elongate in the midventral gap; 20–30 with paired or single markings presetally mostly in the interval *aa*. Only the markings in 11, 17 and 18 are present on the paratypes but these correspond to those found in the holotype.

Internal anatomy. Body has much opaque mucus internally. Septa: none especially thickened. Gizzard: long muscular barrel in 5 (septum 5/6 can be traced to base of gizzard). Oesophagus: not especially dilated, valvular in

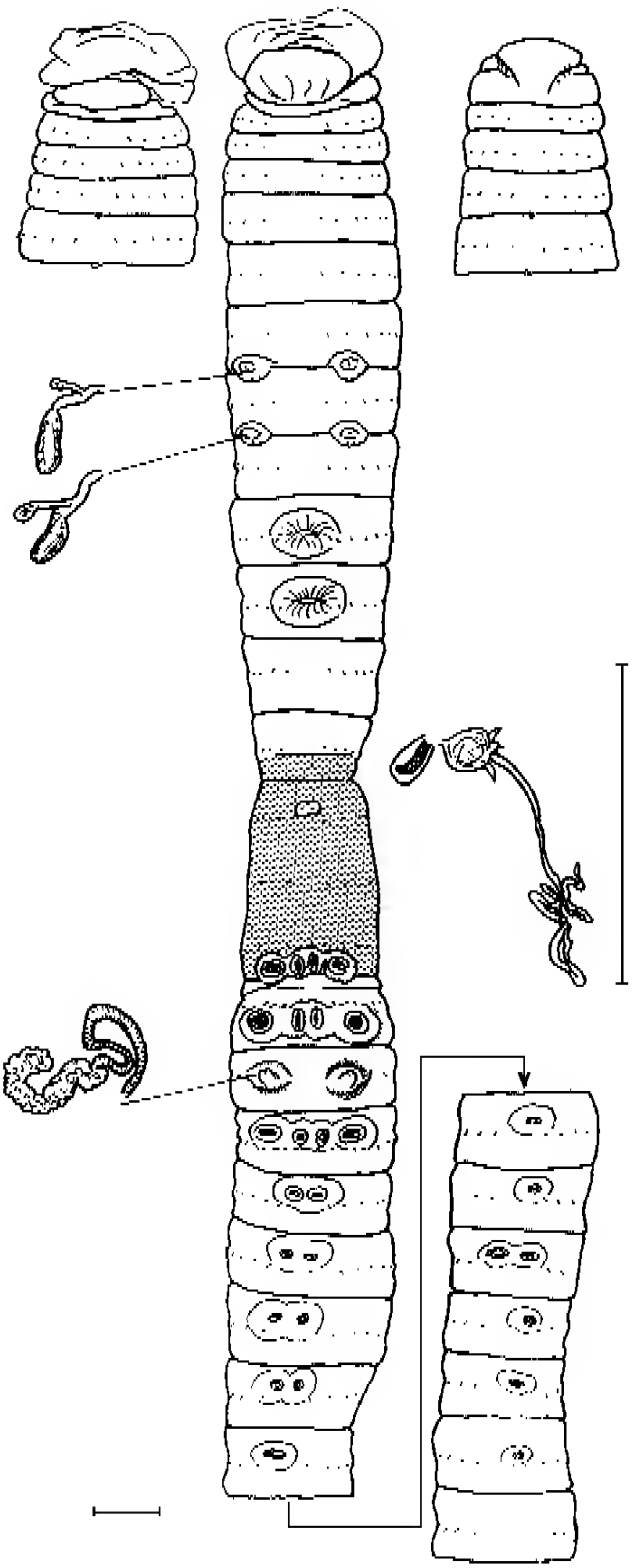

Figure 23. *Anisochaeta toonumbari* ventral view of holotype with dorsal view of prostomium of H and P1 (pharynx everted in H), spermathecae, and lhs prostate in 18–19 with long duct; also shown is enlargement of nephridium with terminal bladder near *h* or *i* seta on rhs in segment 8.

15. Nephridia: vesiculate meroic, tufted in 4 and 5, thereafter smaller tubules with intermittent bladders immediately below seta (in H small bladders seen below *a* and *c* setae in 6 and *c* seta in 7; in P1 seen near *d* and *i* setae in 7–9), after clitellar segments tubules reduce in size and number (about five or six per side) those below *a* or *b*, and *c* or *f*, and *g* or *h-i* setae usually with small sub-spherical bladders; i.e., usually with three small bladders per side; funnels not found. Vascularization: dorsal vessel single onto pharyngeal mass in 4; large hearts in 10–12 from weak supra-oesophageal vessel in 8–12. Spermathecae: in 8 and 9, elongate ampulla on equally long duct joined near midlength or more anteriorly by medium sized diverticulum. Male organs: holandric, seminal vesicles elongate in 9 and 12, iridescent testes and funnels free in 10 and 11. Ovaries: thin and sheet-like with large oocytes in 13; small ovisacs in 14. Prostates: narrow tubuloracemose in 18–19 (tubular with incised gland that in section (H and P1) have narrow central duct with fine side branches), duct long and thin; penial setae absent. Intestine: origin 16; thin lamellar typhlosole develops from 19; gut contents grey sandy soil.

Remarks. *Anisochaeta toonumbari* has vesiculate meronephridia, as do *A. aemula, A. lavatiolacuna*, and *A. yabbratigris*. Postclitellar genital markings are most developed in the holotype compared to the other specimens where markings are found only in 11, 17 and 19. Those in 19 are reminiscent of, though differ from, the conjoined markings on this segment in sympatric *A. conspecta* and in *A. rodwayi*. The distinguishing features of *A. toonumbari*, in addition to the nephridial bladders, are the genital markings: sucker-like in 11, lateral in 17 and 19; the elongate, spermathecae and prostates; and the thin typhlosole.

Etymology. The species epithet is formed from the word "Toonumbar".

Distribution and habitat. Toonumbar and Richmond Range State Forest; found with *A. conspecta* at the second locality.

Anisochaeta tunicata n.sp.

Fig. 24

Material examined. HOLOTYPE: AM W24472, (H), Tree Fern Valley, New England National Park, NSW, c. 30°30'S 152°30'E, 17.iii.1983, Ed Easton, "Jar 15 Sp 31" (mature, posterior amputee, figured and dissected). PARATYPES: ANIC RB.98.2.27, (P1), same details as H (mature, dissected); AM W24474, (P2), same details as H, (aclitellate subadult missing tip of tail).

External features. Lengths (mm): 70+ (H), 87 (P1), 55+ (P2). Width: about 3 mm. Segments: 109 (P1). Colour: anterior and dorsum grey-brown in alcohol with darker mid-dorsal line on paler hind-body; clitellum orange. Prostomium: wide epilobous; peristomium ventrally cleft. Clitellum: ½13 to ½17, weaker ventrally. Dorsal pores: 3/4 small, from 4/5 open. Setae: 20 throughout. Nephropores: not found. Spermathecal pores: in 7/8/9 in or near *b* lines. Female pores: closely paired on 14. Male pores: at centres of large, dark and slightly sunken patches within lateral slits covered by small flaps that hinge laterally. Genital markings: paired presetal markings in 8 (weakly in H only), 9–13 (all specimens) converging from approximate line of spermathecal pores to *a* lines posteriorly; on 18 small indistinct patches may occur anterior to male pores; on 19 paired ill-defined pads within darker patches presetal and just lateral to interval of male pores.

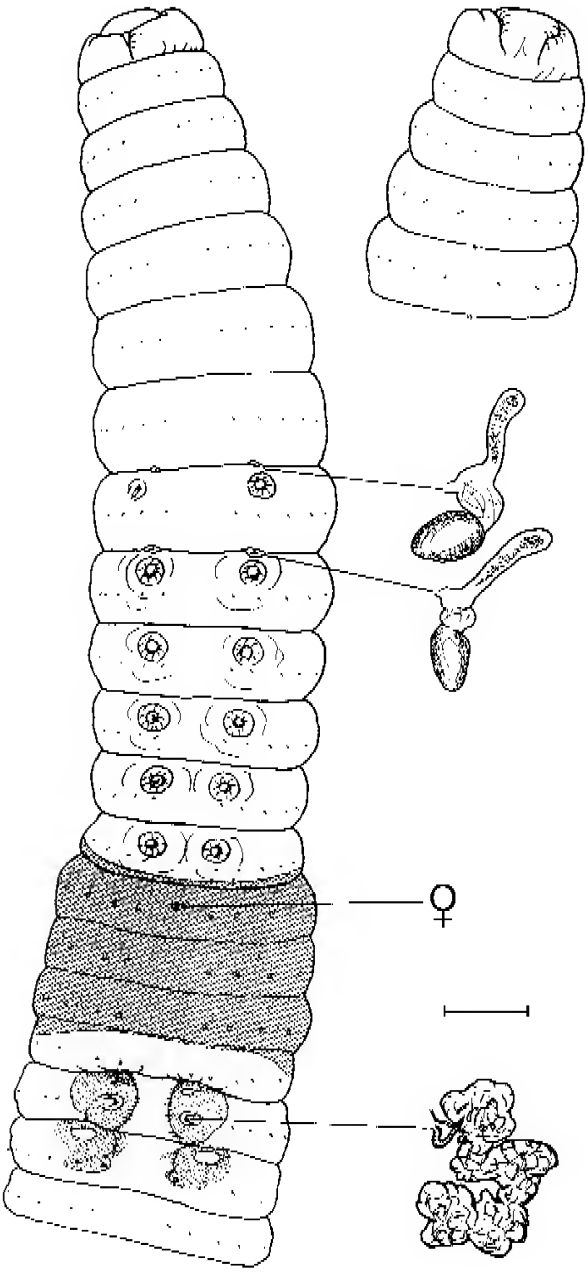

Figure 24. *Anisochaeta tunicata* ventral view of holotype with dorsal view of prostomium, spermathecae, and rhs prostate in 18–19 with vas deferens.

Internal anatomy. Septa: none thickened especially, septum 5/6 thin and displaced dorsally. Gizzard: in 5 and possibly part of 6, (septum 5/6 attaches to top third of gizzard and can only be traced, with difficulty, for about another third; septum 6/7 at base of gizzard). Oesophagus: with regular dilations 8–14, valvular in 15. Nephridia: avesiculate meroic, tufted in 5 and

6, then become bands of thick but short tubules on body wall, smaller after clitellum with approximately one or two at site of each seta except ventralmost where none seen; bladders and funnels not found. Vascularization: dorsal vessel single onto pharyngeal mass in 4; large hearts in 10–12 from large supra-oesophageal vessel in 8,9–13. Spermathecae: 8 and 9, conical ampulla on equally long duct that is dilated in middle opposite where long diverticulum joins. Male organs: holandric, seminal vesicles in 9 and 12, iridescent testes and funnels free in 10 and 11. Ovaries: long palmate in 13; small ovisacs in 14. Prostates: thickly tubuloracemose in 18–19 on short duct, penial setae absent. Intestine: origin 16; deep lamellar typhlosole develops from 20; gut contents dark organic soil.

Remarks. *Anisochaeta tunicata* is morphologically similar to *A. bulla* and both species have rows of genital markings in the anterior. Although these are single and mid-ventral in *A. bulla*, it is possible that the paired markings in *A. tunicata* are analogous. Unique features of *A. tunicata*, apart from the genital markings, are the shape of the spermathecae and the flaps covering the male pores.

Etymology. *Tunicatus*: wearing a tunic—a reference to markings resembling a buttoned, double-breasted jacket.

Distribution and habitat. Tree Fern Valley, New England National Park.

Anisochaeta virgata n.sp.

Fig. 25

Material examined. HOLOTYPE: AM W24475, (H), Tree Fern Valley, New England National Park, NSW, c. 30°30'S 152°30'E, 17.iii.1983, Ed Easton, "Jar 15 Sp 31" (mature, slightly damaged dorsally in 20–21, figured and dissected). PARATYPE: ANIC RB.98.2.30, (P), same details as H (subadult, dissected).

External features. Lengths (mm): 80 (H), 50 (P). Width: 4 mm. Segments: 88 (H and P). Colour: anterior dorsum dark iridescent gun-metal grey, postclitellum dark but setal rings paler to give distinct transverse striped appearance, dark mid-dorsal line also present. Prostomium: open epilobous; peristomium ventrally cleft. Clitellum: ½13–16. Dorsal pores: small dot in 5/6, open from 6/7. Setae: about 30 on 12 and 20, about 48 on tail. Nephropores: not found. Spermathecal pores: widely paired in 7/8/9 in *g* lines. Female pores: paired on 14. Male pores: widely paired on 18 as lateral lipped openings at centres of concentrically wrinkled large pads surrounded by a white rim almost filling segment in *b-e* lines (in P male pores are simple in *cd* lines); no setae intervene. Genital markings: on 10, paired presetal discs in *d* lines (H and P); paired sunken pits with smooth dark discs at centre in 17 postsetally and 19 presetally in *b-e* lines within white rims (H only, P lacks these markings).

Internal anatomy. Septa: none especially thickened. Gizzard: in 5, compact muscular barrel displaced to occupy width of segment 6. Oesophagus: linear narrow, 6–14. Nephridia: avesiculate meroic, not tufted in anterior, as numerous parietal tubules; funnels not found. Vascularization: dorsal vessel single onto pharyngeal mass; hearts large in 10–12 with connective to weak supra-oesophageal vessel. Spermathecae: paired in 8 and 9, ampulla pear-shaped on short duct with long diverticulum ectally. Male organs: holandric, seminal vesicles in 9 and, larger, in 12, iridescent testes and funnels in 10 and 11. Ovaries: palmate with numerous strings in 13; ovisacs paired in 14. Prostates: widely tubuloracemose or racemose in 18–20, penial setae absent. Intestine: suddenly in 15; typhlosole absent; gut contents at anterior of large dead leaf fragments and organic matter, further back this material is compressed. (The paratype agrees internally except that the reproductive organs are less developed).

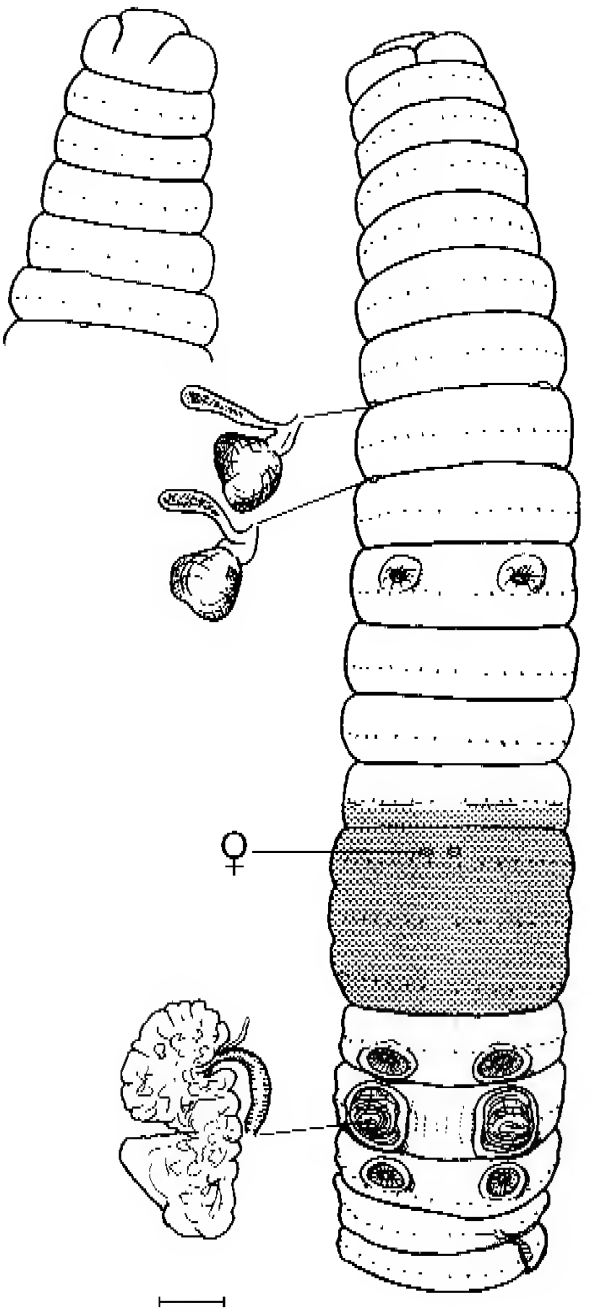

Figure 25. *Anisochaeta virgata* ventral view of holotype with dorsal view of prostomium, spermathecae, and lhs prostate in 18–20 with vas deferens.

Remarks. *Anisochaeta virgata* is similar to *A. aemula* and *A. garilarsoni* (e.g., quadrithecal, lacking calciferous glands and having similar shaped spermathecae and prostates). Major differences in *A. virgata* are more lateral spermathecal pores, and exact arrangements of genital markings. Moreover, *A. aemula* has lateral nephridial vesicles, and glands associated with its markings in 17 and 19; while *A. garilarsoni* has fewer setae, and flaps associated with its male pores. The wide spermathecal pores and distinctive male field are unique characters of *A. virgata*.

Etymology. *Virgatus*: striped.

Distribution and habitat. Tree Fern Valley, New England National Park.

Anisochaeta yabbratigris n.sp.

Fig. 26

Material examined. HOLOTYPE: AM W24554, (H), Yabbra State Forest, NSW, c. 28°30'S 152°40'E, collected 15.iii.1992, M. Gray & D. Charley, pit trap sample set 27.ii.1992, "2BG Trap 13 FN 5012" (mature, figured and dissected). PARATYPES: ANIC RB.98.2.57, (P1), same location as H but "Trap 15 FN 5104" (mature, dissected); AM W24555, (P2), same details as H, but collected 2.iv.1992, set 15.iii.1992 "Trap 14, FN5113" (mature).

External features. Lengths (mm): 58 (H), 52 (P1), 50 (P2). Width: about 2 mm. Segments: 80 (H, P1, P2). Colour: anterior dorsum red-brown with darker mid-dorsal line that persists to tail, pigment lighter after clitellum but setal arc pale to give distinct striped appearance; clitellum buff. Prostomium: open epilobous; ventrally cleft. Clitellum: ½13–16. Dorsal pores: from 5/6. Setae: small, about 24 on 12 and 20, increasing to 30 in midbody and up to 40 on tail. Nephropores: not found. Spermathecal pores: in 6/7/8/9 small pores lateral in *f* lines. Female pore: single on 14. Male pores: widely paired on low mounds that extend from *c* to *e* lines; setae *a* and *b* retained between pores. Genital markings: small presetal discs: on 7 and 8 in *bc* lines and on 17 and 19 *b,c-d* lines (in all specimens, although in P2 that on 19 on rhs only).

Internal anatomy. Septa: none especially thickened. Gizzard: weakly muscular in 5 (barely wider than pharynx). Oesophagus: pale and thin 6–12, dilated and vascularized 13 and 14 but not calciferous, valvular in 15. Nephridia: vesiculate meroic, not tufted, several (about ten per side) small tubules at anterior and equator of segments, with three or four small rounded bladders near some setae (i.e., associated with every second or third equatorial neprhidium); reduced in size after clitellum. Vascularization: dorsal vessel single; small hearts in 10–12 from weak supra-oesophageal vessel. Spermathecae: in 7, 8 and 9, spherical or oval ampulla on equally long duct joined ectally by medium sized diverticulum. Male organs: holandric, seminal vesicles in 9 and 12, iridescent testes and funnels free in 10 and 11. Ovaries: fan-shaped in 13; small ovisacs in 14. Prostates: racemose with three lobes in 18–19, duct branches externally to each lobe; penial setae absent. Intestine: origin 16; typhlosole absent; gut contents organic debris.

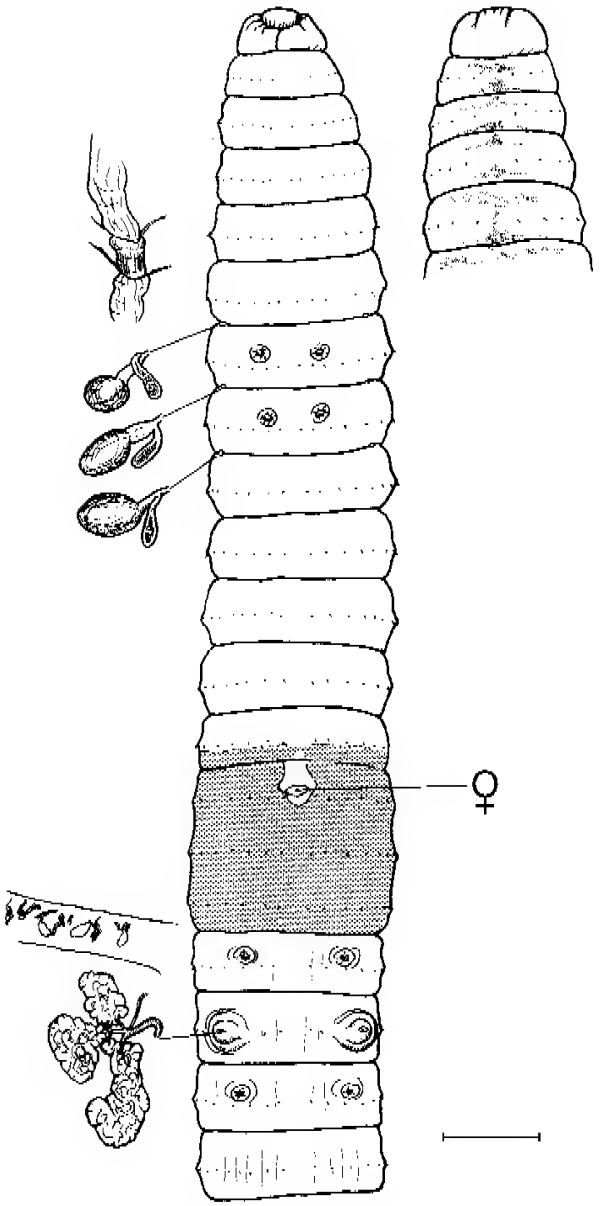

Figure 26. *Anisochaeta yabbratigris* ventral view of holotype with dorsal view of prostomium, weak gizzard in 5, spermathecae, nephridial arrangement on lhs in 17, and lhs trilobed prostate in 18–19 with vas deferens.

Remarks. *Anisochaeta yabbratigris* has three pairs of widely paired spermathecal pores, lacks calciferous glands and has setae median to male pores. These characters are shared with *A. gracilis*, although this species is larger, has different arrangement of male pores and markings, has paired female pores and an intestinal origin in 17, amongst other differences. Distinctive characters of *A. yabbratigris* are the genital markings, vesiculate meronephridia and trilobed prostates.

Setae between the male pores and clitellum restricted to 14–16 are key characters of *Propheretima*. Because the clitellum in *A. yabbratigris* extends ½13–16, it does not qualify for that genus.

Etymology. The name is for a worm from Yabbra State Forest striped like a tiger.

Distribution and habitat. Yabbra State Forest, sympatric with *A. angusticlavia* and *A. calpetana*, as well as other (currently undescribed) congeneric species.

Genus *Propheretima* Jamieson, 1995

Propheretima Jamieson, 1995: 589–590; Blakemore, 1997b: 1839–1843, table 3.

Diagnosis (after Jamieson, 1995: 589). Perichaetine; setae numerous per segment; a few present between the male pores. Female pore single, midvental (or sometimes, *P. hugalli*, paired but very close together). Clitellum (presumably at maximum development), limited to 14–16. Gizzard in 5 (or "virtually vestigial" between 4–6). Calciferous glands present or absent. Intestinal caeca absent. Testes in 10 and 11. (Meroic. Prostates tubuloracemose or racemose).

Type species. *Propheretima eungella* Jamieson, 1995: 590–592, figs. 16,17, from Queensland., (probably a junior synonym of *Perichaeta newcombei* Beddard, 1887—see Blakemore, 1994: 506–510, fig. 2.26; 1997b: 1839–1843, fig. 18).

Distribution. Queensland, northeastern NSW.

Remarks. For a review of *Propheretima*, see Blakemore (1997b). The combination of characters distinguishing this genus from *Spenceriella* (now *Anisochaeta*) was stated by Jamieson (1995:590) to be: presence of setae between the male pores, restriction of clitellum to 14–16 and, "typically", a single female pore. However, several *Anisochaeta* species are known to have setae between the male pores (e.g., *A. gracilis* and *A. yabbratigris* in the current account), as well as *A. notabilis* (Spencer, 1900)—the type-species of *Spenceriella*, see Blakemore (1997b: 1839), *Anisochaeta conondalei* (Jamieson, 1995) and, possibly, *A. indissimilis* (Fletcher, 1889) and *A. illidgei* (Spencer, 1900). Single female pores were found in most, but not all, species formerly placed in *Gemascolex* (now *Anisochaeta*) and are characteristic of several other *Anisochaeta* species (including *A. conondalei*), or they may vary intraspecifically from single to paired (as noted for *A. ancisa, A. calvasaxea, A. lavatiolacuna, A. liberalis* above). Thus the only character remaining for qualification in *Propheretima* is having the clitellum (presumably when the animal is in full breeding condition) restricted to 14–16. However, the exact extent of the clitellum varies intraspecifically, depending on the physiological state of the specimen, on the method of preservation, and on the clarity with which its limits can be defined. Moreover, having the clitellum restricted to, or best developed in 14–16 is found in several *Anisochaeta* species, not least *A. notabilis*, (see Spencer, 1900: 57, fig. 76) as well as *A. conondalei* (see Jamieson, 1995: 594, fig. 20).

Unless further justification for its separation can be found, *Propheretima* should be synonymized in *Anisochaeta*. Nevertheless, the following species is tentatively referred to *Propheretima*, rather than *Anisochaeta*, pending further investigation.

Propheretima monsmonitionis n.sp.

Fig. 27

Material examined. HOLOTYPE: AM W24500, (H), Summit Path, Mt Warning, NSW, c. 28°24'S 153°16'E, 730 m, 26.iii.1992, Ed Easton, "Jar 32 Sp 8" (weakly clitellate mature, figured and dissected). PARATYPES: none.

External features. Length 98 mm. Width: about 2.5 mm. Segments: 106. Colour: anterior dorsum dark grey, after clitellum brown to flanks with pale intersegments, ventrum pale; clitellum buff. Prostomium: widely open epilobous, almost tanylobous; peristomium ventrally cleft. Clitellum: weak defined, 14–16. Dorsal pores: small in 4/5, open from 5/6. Setae: small and dark, about 30 on 12 and 20, increasing to about 50 on tail. Nephropores: not found. Spermathecal pores: small in 7/8/9, just lateral of *d* lines. Female pore: single on 14. Male pores: paired in *c* lines on small mounds; setae *a* retained between pores. Genital markings: small presetal discs on 7–13, 17, 19–22, plus a postsetal pair in 17, mainly paired but irregularly distributed (see figure); small ancillary discs just anteromedian to spermathecal pores on 7 and 8.

Internal anatomy. Septa: none especially thickened. Gizzard: weakly muscular in 5 (barely wider than non-muscular pharynx in 4 and oesophagus in 6). Oesophagus: increasingly dilated in 6–10, in 11–13 paired lateral pouches form sessile calciferous glands with internal rugae; narrower 14–15. Nephridia: avesiculate meroic, dense tubules in 5 resemble tufts, then spread more laterally but still with dense clusters ventrally (at least in 9, 12–16), after clitellum smaller, diffuse, lateral tubules only; funnels not found. Vascularization: dorsal vessel single onto pharyngeal mass in 4; small hearts in 10–12 from weak supra-oesophageal vessel in 10–13 that also supplies calciferous glands. Spermathecae: in 8 and 9, small spherical ampulla tapers to duct with equally long diverticulum ectally. Male organs: holandric, seminal vesicles racemose in 9 and 12, iridescent testes and funnels free in 10 and 11. Ovaries: palmate in 13; small ovisacs in 14. Prostates: flattened racemose in 18, duct curved; penial setae absent (but can see setae *a* and pores of *b* median to where ducts enter body wall). Intestine: origin 16; typhlosole absent; gut contents organic matter.

Remarks. Within *Propheretima* as currently defined, *P. monsmonitionis* is perhaps closest morphologically to *P. newcombei* (Beddard, 1887) differing, at least, on the distribution of genital markings, which, although numerous, are not mid-ventral at any locus in the current species. *Propheretima monsmonitionis* differs from *Anisochaeta* species in the current account that have 2 pairs of spermathecae and 3 pairs of calciferous glands, i.e., *A. australis* and *A. tenax*, by having a weaker gizzard, spermathecal pores more lateral, and more extensive genital markings.

Etymology. After Mt Warning locality.

Distribution and habitat. Mt Warning, found with several other species including *Fletcherodrilus fasciatus* (Fletcher, 1890) (specimen AM W24494 ex "Jar 31, Sp 22"), *Digaster*

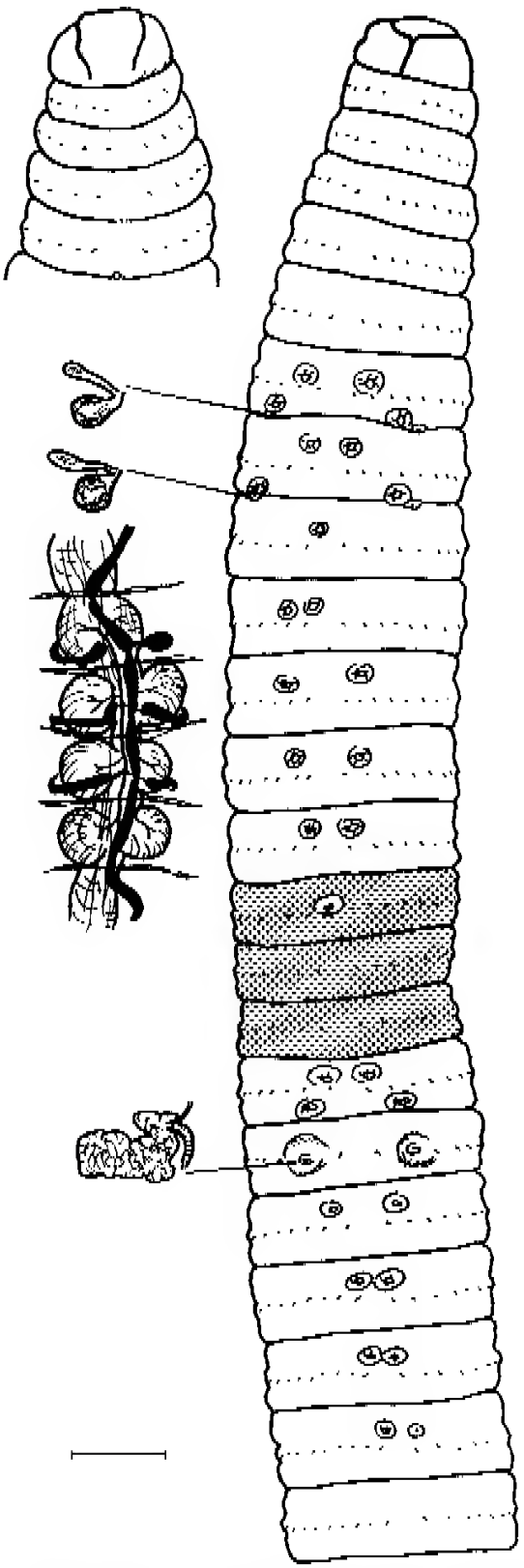

Figure 27. *Propheretima monsmonitionis* ventral view of holotype with dorsal view of prostomium, spermathecae, oesophagus in 9–14 showing vascularization and three pairs of lateral calciferous pouches in 11–13, and lhs prostate in 18.

lamingtonensis Michaelsen, 1916 (specimens AM W24496 ex "Jar 31, Sp 19"); various undescribed *Propheretima* or *Anisochaeta* spp. different to *P. monsmonitionis* (AM W24501, AM W24502 ex "Jar 30, Sp 31"); *Digaster* n.sp. and *Heteroporodrilus* n.sp. Species of these latter two genera will be reported on in a forthcoming paper (Blakemore, in prep.).

Discussion

"It is a matter for comment that the native forms recorded belong, without exception, to the genus *Megascolex* [= *Anisochaeta*], despite the fact that the material examined represents the fruits of much intensive collecting." This observation by Boardman (1943: 168) in introduction to his study of earthworms from the Jenolan Caves region of NSW is pertinent to the findings of the current study. The present samples were mostly from northeast NSW, yet the majority of specimens also belong in *Anisochaeta*. Much of the material examined herein was generated from the survey conducted by Ed Easton during March–May, 1983. Although primarily sorted by him into morpho-species, a single sample of 35 mature and 35 juvenile specimens: "Jar 15 Sp 31" from "Face Fern Valley" (most likely a transcription error for Tree Fern Valley), New England National Park, consisted of ten *Anisochaeta* taxa, nine of these known only from this location, as listed under the account of *A. ancisa* above. This indicates the exceptional diversity and endemicity of native earthworms in this region of NSW. Unfortunately, no details of Easton's collecting methods are available and it is not known whether or not he also found exotic species. However, the material from other studies in the New England region reported here (e.g., Washpool and Yabbra forests) that were previously sorted only to group, did not contain exotic species. In contrast, the more populated Blue Mountains region commonly yields exotic species along with natives in samples (see Fletcher's accounts; Michaelsen, 1907a; Boardman, 1943). Because the region around Sydney has generally been more intensively researched, its importance as a centre of endemicity tends to be over emphasized.

While our knowledge of the diversity and distribution of Australian earthworms, not least of the genus *Anisochaeta* in NSW, is far from complete, clear patterns are emerging. The native fauna of Australia comprises approximately 350 described species in 30 genera. *Anisochaeta* appears particularly speciose with around 100 taxa now known, 50 of these from NSW, yet several species are still not fully resolved and many more undoubtedly await discovery and description. Although most *Anisochaeta* spp. have restricted distributions, reports indicate some have acquired greater ranges via fluvial or human-mediated transportation. Thus, *A. exigua murrayana* occurs from the Riverina region of NSW and Victoria to near the mouth of the Murray River in South Australia; *A. tenax* from Sydney has been reported by Michaelsen (1900) from the Marquesas Islands; *A. macleayi* appears widespread in NSW (Blakemore & Elton, 1994); while *A. sebastiani* was described from Queensland, NSW and Tasmania. Another species, *A. dorsalis* (Fletcher, 1887b), is particularly widespread in Victoria and South Australia as well as in Tasmania (Blakemore, in. prep.).

The difficulties with identifying earthworms when the full extent of the fauna is relatively poorly known, frequently leads to misidentification. Often new native species are ascribed to the morphologically closest classical taxon, falsely extending its frequency and distribution beyond the probable ranges. Exotic species have frequently been similarly confused, for example, *Lumbricus terrestris* Linnaeus 1758 has, in the past, attracted many unverified reports (see Blakemore, 1997a). Undocumented in the current paper are the many samples in the Australian Museums Easton collection labelled "*Megascolex* cf. *monticola*". My preliminary inspection of batches of these (samples between AM W20775 and AM W24357) revealed that they comprised several species, none of which may actually be *A. monticola*. The task of describing these specimens is left to another day.

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Review of the Family Sphaeriidae (Mollusca: Bivalvia) of Australia, With the Description of Four New Species

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ABSTRACT. The sphaeriid fauna of Australia includes 17 species and subspecies, seven of them belonging to *Musculium* and ten to *Pisidium*. Subgeneric classification of *Sphaerium problematicum* Gabriel and identity of *Cyclas egregia* Gould are not defined. Most of the species are endemic, but one species found near Adelaide is probably an introduced *Musculium lacustre* (Müller). All native *Musculium* species are allotted to the subgenus *Sphaerinova*; three subgenera of *Pisidium* are represented (*Afropisidium* and *Odhneripisidium* by one species each and *Euglesa* by eight species). Two anatomically distinct and probably monophyletic groups are distinguished in *Euglesa*. Four species are described as new: *Musculium quirindi* n.sp., *Pisidium (Odhneripisidium) australiense* n.sp., *P. (Euglesa) ponderi* n.sp. and *P. (E.) centrale* n.sp. Descriptions of shell and anatomy as well as the data on distribution and ecology are given for each species and an identification key is provided. Some phylogenetic and zoogeographical implications are discussed.

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The family Sphaeriidae includes the smallest freshwater bivalves (length of adult shell is from 2 to 20 mm). The group is distributed worldwide and inhabits almost all types of freshwater habitats including those (springs, small creeks and peat bogs) where no other bivalves can survive. Therefore, its investigation is important for not only understanding the structure and history of the fauna, but they may be also used in monitoring environmental conditions in some countries. At the same time, sphaeriids remain a group poorly studied in faunistic and taxonomic aspects because of their small size, cryptic mode of life (in bottom sediments) and scarcity of reliable diagnostic characters.

The first sphaeriid named from Australia, *Cyclas egregia*, was described by Gould (1846), but this species has remained dubious until now. The group was reviewed last century in Tasmania by Tenison Woods (1876) and checklisted for the whole continent by E.A. Smith (1883). South Australian and Victorian sphaeriids were reviewed in the 1930's (Cotton & Godfrey, 1938; Gabriel, 1939). Several poorly described species and a genus from New South Wales were added by Iredale (1943b). The list of Australian freshwater molluscs published in the same year (Iredale, 1943a) included 16 species of Sphaeriidae allotted to three endemic genera. Another species from South Australia was described by Cotton (1953).

Iredale and Cotton regarded the Australian sphaeriid fauna as endemic at the generic level and rather diverse. Most of the species were attributed to limited geographic areas. However, these authors failed to provide reliable diagnostic characters and their work has been strongly

criticised by later authors (B.J. Smith & Kershaw, 1979; Kuiper, 1983). As a result, in some field guides on freshwater molluscs (B.J. Smith & Kershaw, 1979, 1981) the opposite point of view was proposed: only two species of the common genera *Sphaerium* and *Pisidium* were recognised, one of them being the supposedly cosmopolitan *Pisidium casertanum* (Poli, 1791).

The most recent revision of Australian sphaeriids was published by Kuiper (1983), who recognised 12 species (three of them described as new). All the species were included in the widely distributed genera *Pisidium* and *Sphaerium*, the latter with an endemic subgenus *Sphaerinova* Iredale, 1943a. Most of the species (five *Sphaerium* and six *Pisidium*) were considered endemic; one species was identified as *P. casertanum*, a taxon widely distributed outside Australia. Kuiper's view on the group was accepted recently by B.J. Smith (1992).

Different views on the origin of the Australian fauna of sphaeriids have been published. McMichael (1967) and Starobogatov (1970) regarded it as derived from south Asia. Kuiper (1983) suggested ancient, Gondwanan origin for some Australian taxa. In the zoogeographic reviews of B.J. Smith & Kershaw (1979) and Taylor (1988), Australian sphaeriids were neglected because of insufficient knowledge of their affinities.

Despite sphaeriid research in Australia having a rather long history, many aspects of the systematics, biology and biogeography of the group need much further investigation. The status of some species and forms is not settled and there are considerable gaps in outlining distributions. Affinities of Australian taxa to each other and to those known from the other continents are poorly studied.

Since 1983, extensive collecting was carried out by the staff of the Australian Museum, Sydney in areas previously poorly studied (Northern Territory, northern Queensland, central Tasmania). Numerous samples of sphaeriids were preserved in alcohol or formalin and were consequently available for anatomical study and statistical assessment. In addition, some new sphaeriid collections were accumulated in the other Australian museums.

Quite recently, new anatomical data were obtained and successfully used for taxonomy and phylogenetic analysis of sphaeriids from different regions (Korniushin, 1992, 1995, 1998a; Dreher-Mansur & Meier-Brook, 1992). The anatomical investigation of Australian sphaeriids is of importance for understanding both the evolution of the group at the global scale and the history of the Australian freshwater fauna. Characters of shell microsculpture, especially those of shell pores, regarded as taxonomically significant by recent investigators (Dyduch-Falniowska, 1983; Kuiper & Hinz, 1984), were also not previously studied in most of the Australian species.

The aim of the present study was to obtain a better understanding of the taxonomic diversity and affinities of Australian sphaeriids by using new material and recently proposed taxonomic characters. Earlier published descriptions and diagnoses are supplemented by anatomical and some microstructural characters and several new species are described. An identification key is provided and some phylogenetic and zoogeographical problems are discussed.

Materials and methods

Material for this study was obtained mainly from zoological museums in Australia: Australian Museum, Sydney—about 250 lots; Western Australian Museum, Perth—8 lots; South Australian Museum, Adelaide—20 lots; Queen Victoria Museum, Launceston—8 lots; Tasmanian Museum, Hobart—about 40 lots. Most of the type specimens deposited in Australian and European museums were revised.

Distribution maps include all localities of the material used in this study. Collection data for the type lots and the other reference lots (those taken for statistical, microstructural or anatomical investigation) are provided, type lots marked with an asterisk (*) were not examined in this study.

The shells were studied by light microscopy and Scanning Electron Microscopy (SEM). Specimens selected for SEM were coated with gold using a Dynavac Mini Coater and examined with a Cambridge Instruments Stereoscan 120 microscope using Secondary Electron Detector and Robinson Detector (for backscatter electrons), at 18KV and a working distance 18–30 mm. When necessary, adherent material was removed from shells by treating with 25% hypochlorite bleach and cleaning by hand.

Pores were counted on SEM photographs. In those, taken at high magnification (400×) counts were made for the whole area covered; several smaller patches were separately observed in each photograph taken at lower magnification (200×). In each case, the area covered by photographing was estimated from the scale bar. Pore density was recalculated for 1 mm^2, mean values and standard deviation are provided in descriptions, when applicable.

The following shell measurements were made (Fig. 1): shell length (L), shell height (H), shell width (W), height of the hinge plate under umbo (HH), length of ligament pit (LL), length of hinge—equivalent to the distance between cusps of lateral teeth in the left valve (LH), distance of umbo from anterior (LA) and posterior (LP) margins. The following indices were calculated: relative shell height (H/L), relative hinge plate height (HH/H), relative hinge length (LL/L), position of the umbo (not in all lots) (LA/LP), relative shell width (W/H). In *Musculium*, the length of the embryonic shell LE was also measured and its relative size (LE/L) was calculated. A total of 450 specimens were measured; specimens from large lots (more than 20 specimens) were selected randomly. Basic statistical parameters (mean value and standard deviation) were calculated for each sample.

All computerised statistical treatments were made using Statistica for Windows including a standard, two-tailed test for independent samples.

Traditional designation of hinge teeth (Kuiper, 1983) is applied here: in the left valve, cardinal teeth are marked as c2 (inner) and c4 (outer), posterior lateral teeth as p3 and anterior laterals as a3; in the right valve, cardinal tooth is c3, posterior lateral teeth are p1 (inner) and p3 (outer), anterior laterals a1 and a3 respectively (see Fig. 1).

Anatomical study was based on methodology used for Palaearctic (Korniushin, 1992, 1996b) and African species (Piechocki & Korniushin, 1994; Korniushin, 1995). Characters of the mantle edge (including musculature), gills

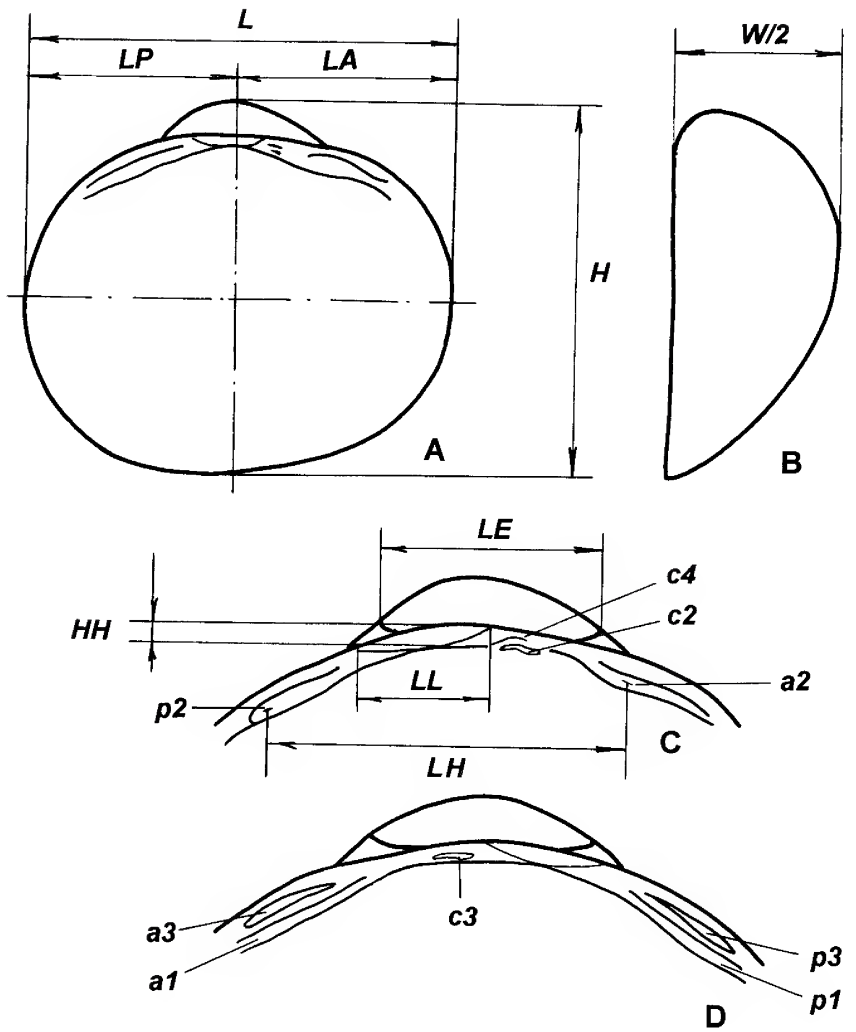


Figure 1. Shell measurements and hinge teeth designations applied in this paper: A—left valve from the inner side; B—the same valve anteriorly; C—hinge of the left valve; D—hinge of the right valve. *L*—shell length, *LP*—length of posterior part of the shell, *LA*—length of anterior part, *LE*—length of embryonic (nepionic) shell, *H*—shell height, *W*—shell width, *c2–c4*—inner and outer cardinal teeth of the left valve, *c3*—cardinal tooth of the right valve, *a1–a3*—inner and outer anterior lateral teeth of the right valve, *p1–p3*—corresponding posterior lateral teeth, *a2*—anterior lateral tooth of the left valve, *p2*—corresponding posterior lateral tooth.

(including brood pouches) and nephridia were investigated. The latter were studied *in situ*, after opening the valves. If the part of proximal duct was observed between the branches of the dorsal lobe, the type of nephridium was defined as open; in nephridia of the closed type the branches tightly adjoin each other (Fig. 2A–C). Gills and mantle were stained with Grenacher's carmine and water eosine respectively and mounted on microscope slides in Canada Balsam. The position of the outer demibranch was evaluated by counting inner demibranch filaments in front of its anterior margin (Fig. 2D, see also Korniushin, 1996a, 1997). Siphons were observed in life, whenever material was available; siphonal retractors were figured from preserved specimens (Fig. 2E). Number, size and arrangement of inner radial muscle bundles were observed in mantle preparations of *Pisidium* species and the other elements of mantle musculature were also taken into account (Fig. 2F). SEM was also used for the study of pallial structures by using critical point drying with a BIORAD CPD750.

Abbreviations of museum collections are as follows; in the text the type of the lot is indicated by the letter d (dry lot) or w (wet alcohol or formalin lot) after the collection number or museum abbreviation:

AM	Australian Museum, Sydney
IZK	Institute of Zoology, Kiev
BMNH	Natural History Museum, London
QVM	Queen Victoria Museum, Launceston
SAM	South Australian Museum, Adelaide
SMF	Senckenbergsmuseum, Frankfurt-am-Main
TMH	Tasmanian Museum, Hobart
WAM	Western Australian Museum, Perth
coln.	a particular collection in the museum, when applicable

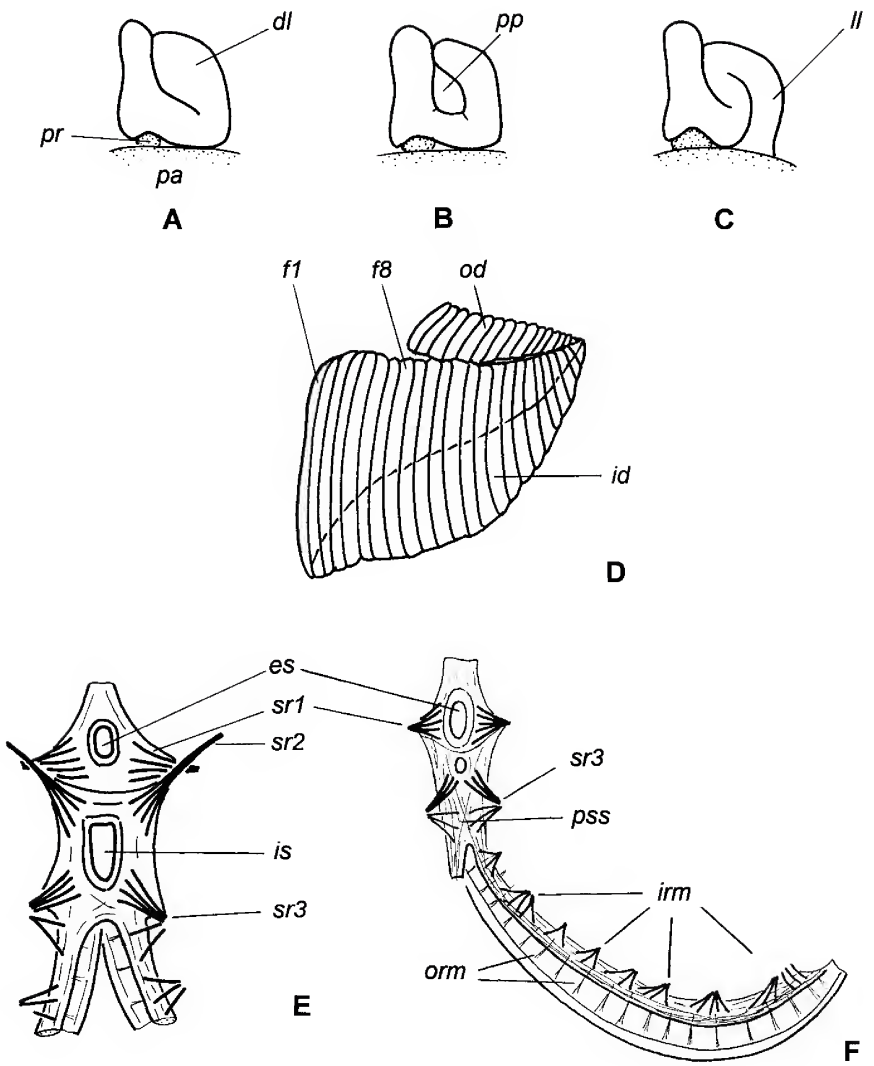


Figure 2. Principal anatomical characters: A–C—types of nephridium (dorsal view): closed (A), open (B), with visible lateral loop (C); D—diagrammatic view of ctenidium from outside, defining of the outer demibranch position (in this case it extends from the eighth filament): *f1*—first filament of the inner demibranch, *f8*—eighth inner demibranch filament, if counted from the anterior edge; E—siphons and siphonal retractors in *Musculium* (diagrammatic internal view); F—mantle edge with its musculature in *Pisidium* (diagrammatic internal view).

Collectors names are abbreviated as follows: AK, A.V. Korniushin; FWA, F.W. Aslin; GC, G. Clark; IL, I. Loch; JH, J. Hall; JW, J. Waterhouse; OG, O. Griffiths; WFP, Winston F. Ponder; WP, Warwick F. Ponder. Abbreviations of states, territories and topographic terms: NSW, New South Wales; NT, Northern Territory; Qld, Queensland; SA, South Australia; Tas., Tasmania; Vic., Victoria; WA, Western Australia; Ck, creek; Hwy, highway; Mt, mountain; NP, National Park; alt., altitude; Rd, road.

Anatomical structures, labelled on the figures:

aa anterior adductor
bp brood pouches
dg digestive gland
es exhalant siphon
g gill
irm inner radial muscles
is inhalant siphon
ldl lateral branch of the dorsal lobe
ll lateral loop
mdl medial branch of the dorsal lobe
orm outer radial mantle muscles
pa posterior adductor
pp pericardial part of nephridium
pr pedal retractor
pss presiphonal suture
sr1 retractors of the exhalant siphon
sr2 dorsal retractors of the inhalant siphon
sr3 ventral retractors of the same siphon
s excretory sac

Systematic account

Genus *Musculium* Link, 1807

Type species. *Tellina lacustris* Müller, 1774, by monotypy.

Distribution. Almost cosmopolitan (all continents except Antarctica).

Diagnosis. Shells usually thin and fragile. Umbones narrow (in comparison with *Sphaerium*), central or slightly shifted posteriorly. Hinge plate relatively narrow; tendency to hinge teeth reduction evident in many (but not all) species. Both siphons tubular. Upper (exhalant) siphon with one pair of retractor muscles, lower (inhalant) with two pairs (Fig. 2E). Outer demibranch of two lamellae, relatively small (height about 1/3 inner demibranch height), begins at 5th filament of inner demibranch (Starobogatov & Streletskaja, 1967; Korniushin, 1996a). Brood pouches multiple. Nephridia with long and narrow funnel and small excretory sac without internal valve (Dreher-Mansur & Meier-Brook, 1992).

Remarks. This genus was for a long time regarded as a subgenus of *Sphaerium*. Generic rank was applied by Starobogatov & Streletskaja (1967), Burch, (1975), Heard (1977), Dreher-Mansur & Meier-Brook (1992) and Korniushin (1996a). Shell characters were not reliable for diagnostics, while in some species they were intermediate between *Musculium* and *Sphaerium* (see also Heard, 1977). Peculiarities of reproduction and life cycle, namely late (in comparison with *Sphaerium*) formation of eggs and sperm, small size of intramarsupial larvae, higher fecundity, high growth rate and short life span were reported by Heard (1977). These characters are associated with the preference for temporary or unstable water bodies, evident in the majority of species. Validity of the genus *Musculium* was confirmed by the study of enzymes (Hornbach, 1980). However, the best generic diagnostic characters were provided by the study of nephridia (Dreher-Mansur & Meier-Brook, 1992). *Musculium* is well distinguished from *Pisidium* by larger size, median or nearly median position of the umbo, presence of two tubular siphons, two pairs of retractor muscles by the lower (branchial) siphon, outer demibranch with two lamellae and multiple brood pouches.

Cyclas tasmanica Tenison Woods, 1876 was first attributed to *Musculium* by Heard (1977). In the present study the diagnostic characters of nephridium were checked, and the diagnostic long funnel and small excretory sac without an internal valve were observed in all Australian species previously included in *Sphaerium s.l.* by Kuiper (1983).

Subgenus *Sphaerinova* Iredale, 1943a

Type species. *Sphaerium macgillivrayi* E.A. Smith, 1882 by original designation.

Distribution. Australian, but may also include taxa from New Zealand, south Asia (India) and South America (see Remarks).

Diagnosis. Shells small (length up to 9 mm, usually 7 to 8 mm) compared with that in nominate subgenus; beaks usually slightly shifted posteriorly, not protruding, prodissoconch sometimes separated by growth break line but never forming bean-shaped cap. Ligament externally visible, elevated in largest specimens. Siphons short, especially their fused part; dorsal retractor muscles of inhalant siphon markedly reduced and scars merged with those of posterior adductors. Outer demibranch 0.3 to 0.4 height of inner demibranch (depending on stage of development).

Remarks. In introducing the genus *Sphaerinova*, Iredale (1943a) distinguished it from *Sphaerium* by the narrow ligament plate and somewhat reduced cardinal teeth. However, these characters are diagnostic of *Musculium* as a whole, not just of the Australian taxa. Kuiper (1983) treated *Sphaerinova* as a subgenus of *Sphaerium* with two species, namely *S. tasmanicum* and *S. lacusedes* Iredale, 1943a, distinguished from *Musculium* (which he considered to be another subgenus of *Sphaerium*) by their externally visible ligament and by the peculiar form of the umbo (no bean shaped caps). B.J. Smith (1992) also accepted subgeneric status of *Sphaerinova* within *Sphaerium s.l.*, but included in this taxon all Australian species of the group.

The placement of *Sphaerinova* in *Musculium* is confirmed by the similarity in shell characters, peculiarities of reproduction (Heard, 1977) and, especially, by the diagnostic characters of the nephridium. Alongside the characters, provided by Kuiper (1983), it is distinguished from the nominate subgenus by the markedly reduced siphonal retractors. Short siphons were found in the two species observed alive (Figs. 6D,E, 19A,B), and the weakness of the retractors suggests that this character is common to all species. The umbo is shifted somewhat posteriorly in many of them.

Australian species observed below are considered consubgeneric because of the similarity in the main characters of the siphons, siphonal musculature and gills. In my opinion, differences in the ligament position between *M. kendricki* and *M. problematicum* vs *M. tasmanicum* and *M. lacusedes* mentioned by Kuiper (1983: 25) are not significant: all species have an externally visible ligament and the degree of its elevation evidently depends on shell size, being most pronounced in large specimens of *M. tasmanicum, M. lacusedes* and *M. tatiarae*.

Musculium novaezelandiae (Deshayes, 1854) from New Zealand is considered closely related to *M. tasmanicum* by many authors (Heard, 1977; Kuiper, 1983), thus it may also belong to *Sphaerinova*. Several anatomically studied species from South America and south Asia are characterised by the posterior shift of the umbo and the external ligament (Kuiper & Hinz, 1984; Subba Rao, 1989) and may be related to or possibly consubgeneric with Australian taxa.

Musculium (Sphaerinova) tasmanicum (Tenison Woods, 1876)

Diagnosis. Shell quadrangular or trapezoid, very thin and fragile, transparent. Upper (dorsal) margin almost straight, with clear angles. Umbones narrow, protruding. Internal

pores dense. Hinge plate narrow, cardinal teeth straight or slightly bent, lateral teeth normally developed.

Shell quadrangular or trapezoid, compressed, thin-walled, transparent, sometimes of red or brown colour due to staining. Dorsal margin straight or slightly curved. Anterior and posterior ends usually markedly angulated. Umbones narrow or moderately broadened, somewhat protruding, sometimes with separated prodissoconch. External surface smooth (Fig. 3C). Internal pores rather abundant (Fig. 3D). Siphonal retractors scars distinguishable but merged to posterior adductor scars. Hinge plate narrow (Table 1), especially under umbo; hinge teeth thin, cardinals straight or slightly bent; lateral teeth straight. Ligament visible from outside, somewhat protruding, ligament pit long and narrow. Shells of young specimens circular or short oval.

Anatomy. Gill and siphonal characters as in subgeneric diagnosis. Inner demibranch with three to four (rarely five) brood pouches, including up to five (usually two or three) filaments each. Nephridium usually of closed type, proportions of dorsal lobe vary.

Distribution. Northern Territory (occasionally); along the east coast and Great Dividing Range from northern Queensland to Victoria; the Murray-Darling system (apparently rare), including South Australia (lower Murray); Tasmania.

Ecology. Appears to show a preference for lentic water.

Remarks. This species is one of the most variable among Australian sphaeriids. Variability of the shell shape, position of umbo and the shape of nephridium (to a lesser extent) shows clear geographical pattern. The northern form is the most distinct in its morphological character and geographically separated from the nominate form widely distributed in the Australian mainland and Tasmania. However, morphological differences between these forms concern only a few characters, and the limits of their variation nearly overlap. Because of the geographic separation without a clear morphological gap, both forms are defined as subspecies.

Table 1. Shell indices in the species of *Musculium* (mean ± SD, N—number of measured specimens, measurements shown in Fig. 1). Abbreviations: N—number specimens measured; H/L—relative shell height; HH/H—relative height of the hinge plate; LL/L—relative length of the ligament pit; LH/L—relative hinge length; LA/LP—position of umbo; LE/L—relative length of embryonic (prodissoconch) shell (not measured in *Pisidium*); W/H—relative shell width.

species and locality	N	H/L	HH/H	LL/L	LH/L	LA/LP	LE/L	W/H
Musculium tasmanicum tasmanicum								
Coomooboolaroo, Qld	3	0.81±0.016	0.21±0.002	0.20±0.008	0.58±0.029	1.23±0.066	0.21±0.023	0.63±0.009
Binnum Waterholes, SA	7	0.80±0.015	0.023±0.008	0.18±0.008	0.55±0.015	1.13±0.068	0.18±0.030	0.64±0.030
Table Cape, Tasmania	5	0.82±0.014	0.020±0.004	0.22±0.019	0.52±0.015	0.94±0.071	0.20±0.019	0.64±0.041
pooled	15	0.81±0.015	0.022±0.005	0.19±0.019	0.56±0.025	1.16±0.079	0.19±0.029	0.64±0.025
pooled, range		0.80–0.84	0.014–0.034	0.18–0.25	0.50–0.61	0.86–1.28	0.14–0.23	0.58–0.69
Musculium tasmanicum queenslandicum								
Atherton Tableland, Qld	3	0.84±0.007	0.019±0.021	0.20±0.021	0.60±0.009	1.25±0.071	0.20±0.027	0.65±0.075
Buffet Creek, NT	7	0.84±0.008	0.022±0.004	0.21±0.015	0.61±0.009	1.30±0.041	0.20±0.029	0.60±0.032
pooled	10	0.84±0.007	0.021±0.004	0.21±0.018	0.60±0.010	1.28±0.053	0.20±0.027	0.61±0.051
pooled, range		0.83–0.86	0.016–0.029	0.18–0.24	0.59–0.63	1.18–1.38	0.17–0.25	0.565–0.74
Musculium tatiarae								
Lake Eliza, SA	5	0.86±0.006	0.043±0.004	0.19±0.011	0.57±0.026	1.04±0.073	0.27±0.044	0.61±0.035
Binnum Waterholes, SA	8	0.84±0.014	0.032±0.008	0.23±0.022	0.59±0.024	1.15±0.103	0.24±0.028	0.64±0.020
Lake Torrens, SA	6	0.84±0.012	0.031±0.006	0.24±0.029	0.59±0.021	1.08±0.063	0.17±0.029	0.67±0.049
pooled	19	0.84±0.014	0.035±0.008	0.22±0.028	0.58±0.024	1.10±0.093	0.23±0.049	0.64±0.041
pooled, range		0.83–0.87	0.018–0.048	0.18–0.28	0.54–0.64	0.96–1.30	0.13–0.32	0.58–0.72
Musculium lacusedes								
pooled	5	0.78±0.038	0.035±0.006	0.20±0.025	—	1.02±0.064	0.25±0.075	0.59±0.029
Musculium kendricki								
north of Capel, WA	5	0.85±0.010	0.033±0.006	0.18±0.020	0.63±0.068	1.15±0.044	0.21±0.019	0.64±0.014
Musculium quirindi								
paratypes	5	0.81±0.014	0.037±0.003	0.19±0.013	0.57±0.016	1.54±0.096	0.21±0.035	0.71±0.034
Attunga, NSW	5	0.86±0.015	0.032±0.007	0.21±0.012	0.58±0.014	1.18±0.058	0.25±0.020	0.75±0.036
pooled	10	0.83±0.027	0.034±0.006	0.20±0.016	0.58±0.015	1.36±0.20	0.23±0.033	0.73±0.041
pooled, range		0.80–0.87	0.022–0.040	0.18–0.23	0.56–0.60	1.13–1.64	0.16–0.27	0.68–0.79

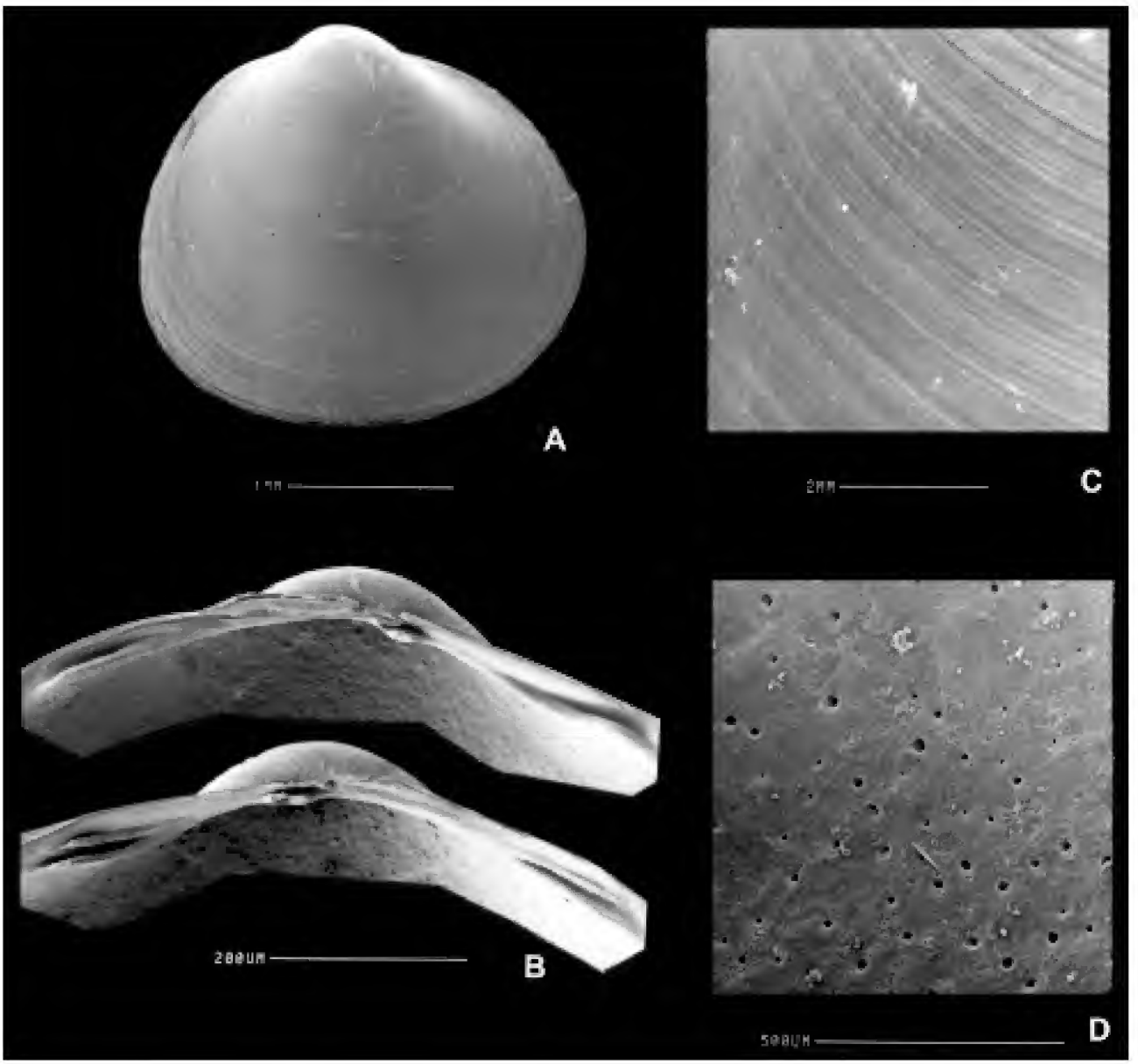


Figure 3. *Musculium tasmanicum tasmanicum* (Tenison Woods), Blue Mountains, NSW (AM, no number), shell: A—exterior view of left valve, B—hinge, C—sculpture, D—internal pores.

Musculium (Sphaerinova) tasmanicum tasmanicum

Figs. 3–8

Cyclas tasmanica Tenison Woods, 1876: 82.
Sphaerium translucidum Sowerby in Reeve, 1876: pl. 5, fig. 46; E.A. Smith, 1883: 305, pl. 7, fig. 32; Iredale, 1943a: 196.
Sphaerium macgillivrayi E.A. Smith, 1883: 305, pl. 7, fig. 34.
Sphaerinova macgillivrayi.–Iredale, 1943a: 195.
Sphaerinova victoriana Iredale, 1943a: 195.
Sphaerinova nundialis Iredale, 1943a: 195; Iredale, 1943b: 95, fig. 3.
Sphaerinova terenda Iredale, 1943b: 95, fig. 3.
Australpera bradena Iredale, 1943a: 196; Iredale, 1943b: 95, fig. 3.
Sphaerium tasmanicum.–Kuiper, 1983:19, figs. 14–29 (part: typical form and forms *terenda, bradena* and *nundialis*).

Type material. Possible syntypes TMH E1111/7452*, a few fragments, Swansea, east coast, Tas., revised by Kuiper (1983). *Sphaerium translucidum*, holotype and 2 paratypes BMNH 1846.10.7.144/145-6, Palmtree Ck, Qld. *Sphaerium macgillivrayi*, syntypes, 1 specimen and 1 valve, BMNH 1859.10.28-9, Penrith, NSW. *Sphaerinova victoriana* Iredale, possible syntypes, NMV F533*, 7 specimens and a valve, Tarraville, Vic., revised by Kuiper (1983). *Sphaerinova nundialis*, lectotype (Kuiper, 1983: 21) AM C109823, Nundle, NSW. *Sphaerinova terenda*, holotype AM C100522 and paratype AM C109821, Leeton, Murrumbidgee River, NSW. *Australpera bradena*, holotype AM C100521, Braidwood, NSW.

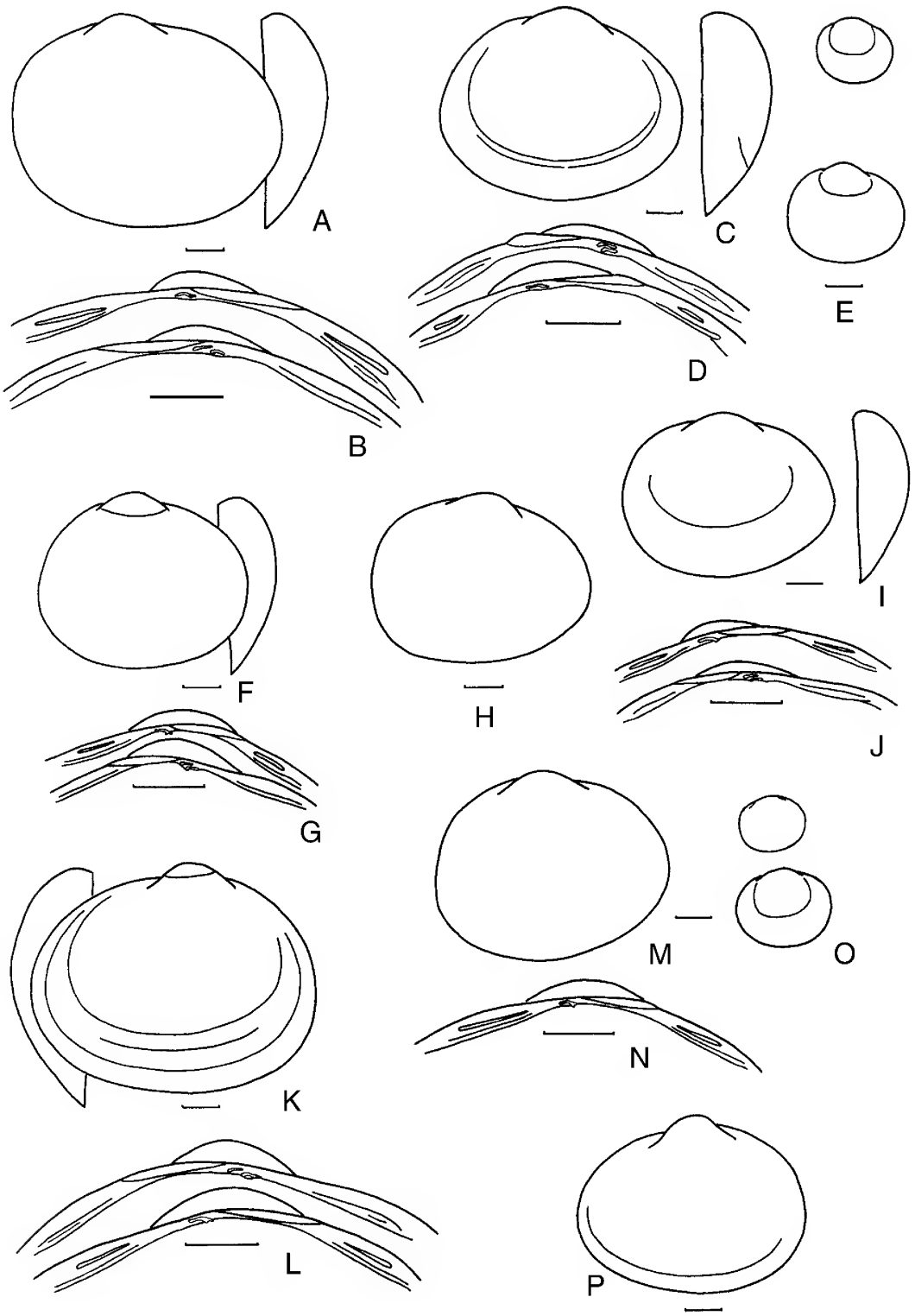


Figure 4. *Musculium tasmanicum tasmanicum*, variation of shell form: A,B—Coomooboolaroo, Qld (AM C109829), A—right valve, here and below the views from outside and hind end are provided, B—hinge; C–E—Somerset Dam, Qld (AM C135527), C—right valve, D—hinge, E—young shells; F,G—Attunga State Forest, NSW (AM, no number), right valve and hinge; H—Dubbo, NSW (AM 02832), right valve from outside; I,J—Tarraville, Vic. (SAM D19061), right valve and hinge; K,L—Binnum Waterhole, SA (SAM D19062), left valve and hinge; M–O—Table cape, Tas. (AM, no number), M—right valve, N—hinge of the right valve, O—young shells; P—Hobart, Tas. (AM C27754), left valve. Scale bars = 1 mm.

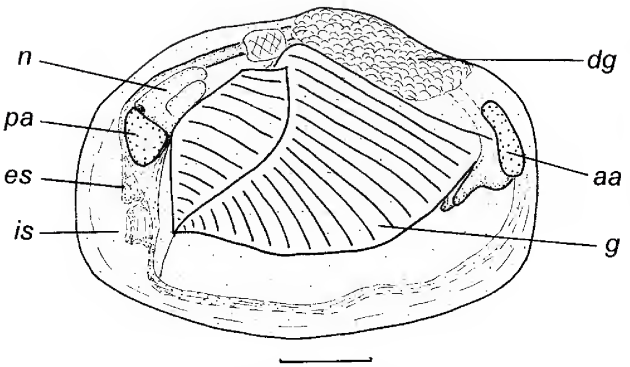
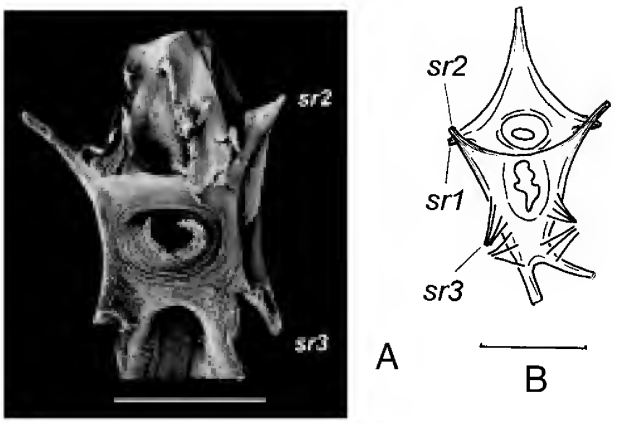


Figure 5. *Musculium tasmanicum tasmanicum*, Somerset Dam, Qld (AM C135527), gross anatomy. Scale bar = 1 mm.



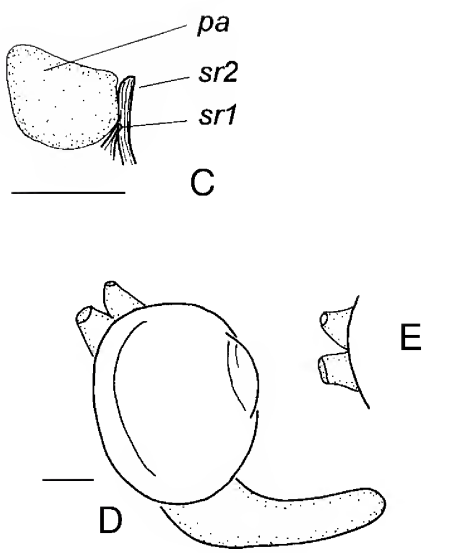
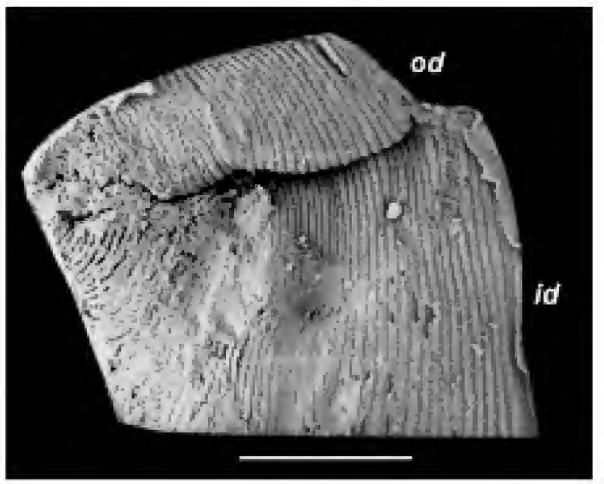


Figure 6. *Musculium tasmanicum tasmanicum*, siphons and siphonal musculature: A—Blue Mountains, NSW (AM, no number), siphons from inside; B—Somerset Dam, Qld (AM C135527), siphonal retractors from inside; C—specimen from the same lot, posterior adductor and adjacent siphonal retractors from right side; D,E—fully extended siphons in living specimens from Blue Mountains, NSW. Scale bars = 1 mm.



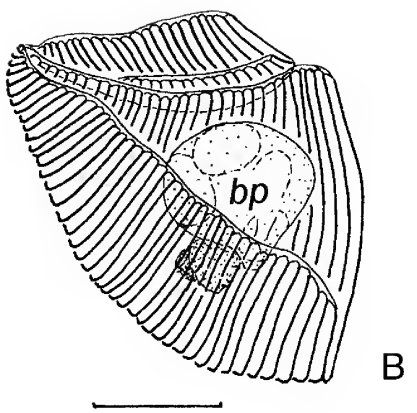


Figure 7. *Musculium tasmanicum tasmanicum*, gills: A—Blue Mountains, NSW (AM, no number), upper part of gill from outside; B—Somerset Dam, Qld (AM C135527), gill with brood pouches from inside. Scale bars = 1 mm.

Other material examined. QUEENSLAND: lagoon at Coomooboolaroo, Mt Duaringa, Dawson District (AM C109829d); east of Somerset Dam, between Mt Byron and Mt Delaney, small weedy muddy stream, coll. WFP, WP & OG, 30 September 1982 (AM C135527w); tributary of Brisbane River, 27°32'S 152°54'E, coll. WFP, WP & OG, 5 September 1982 (AMw). NEW SOUTH WALES: Attunga State Forest, 30°55'S 150°54'E, coll. IL & JW, 9 November 1985, with *M. quirindi* n.sp. (AMw); near Dubbo (AM 02832d); west end of Lake Lidell, 32°23'S 151°08'E, coll. P. McWilliamson, D. Hoese & J. Paxton, 24 November 1972 (AM C129137w); Warranwang, west of Lithgow, Blue Mountains, 33°28'S 149°59'E, on grass, moss, etc., coll. WFP & A. Korniushin, 18 August 1996 (AMw); Bora Ck at Mayfield, 35°13'S 149°47'E, coll. WFP & WP, 12 January 1981 (AM C126457w); Tuross River valley near east end of Cadger Rd, 36°09'S 149°55'E, coll. WFP, 19 January 1981 (AM C128099w); East Lakes Golf Course, Sydney, 33°56'S 151°13'E, coll. OG, 7 August 1982 (AM C315745w). VICTORIA: Tarraville, Gabbriel coln. (SAM D19061d); Loddon River at Newstead, 37°07'S 144°03'E, alt. 220 m, coll. WFP & R. Hershler, 2 February 1984 (AMw). SOUTH AUSTRALIA: Binnum Waterhole Police Paddock, Tatiara Ck, Bordertown, coll. June 1886, Tomsett coln., with *M. tatiarae* (SAM D19062d); Lower Murray River,

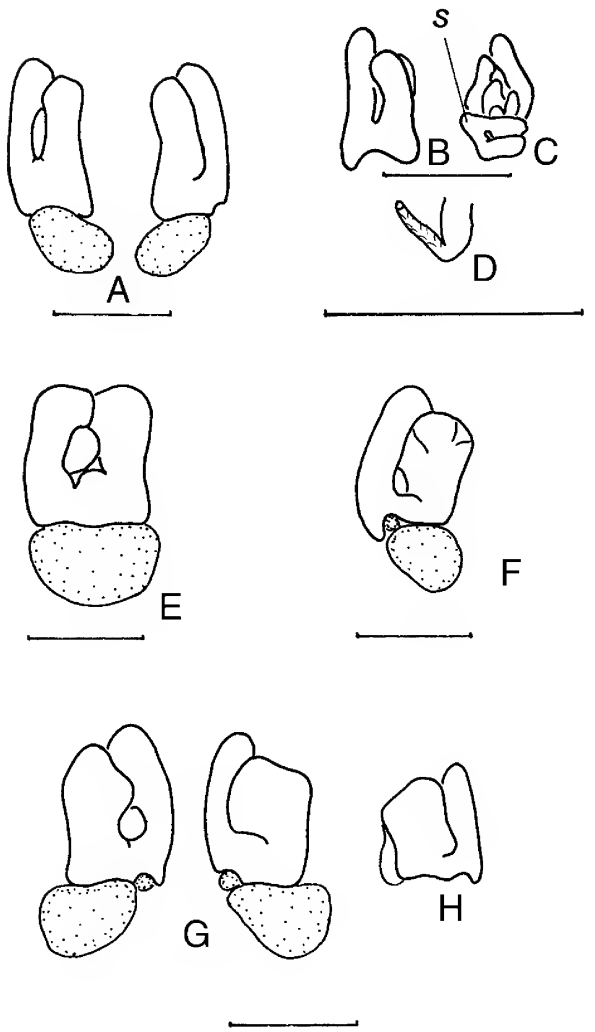


Figure 8. *Musculium tasmanicum tasmanicum*, nephridia: A—Somerset Dam, Qld (AM C135527), dorsal view; B—Brisbane River, Qld (AM, no number), dorsal view; C—ventral view of the same nephridium; D—funnel of the nephrostome of the same nephridium; E—Blue Mountains, NSW (AM, no number), dorsal view; F—Sydney, NSW (AM C315745), dorsal view; G,H—Table Cape, Tas. (AM, no number), dorsal view, two nephridia of one and the same specimen are figured in G. Scale bars = 1 mm.

Tailem, Cotton coln. (SAM D19064d). TASMANIA: swamp on Table Cape, 40°57'S 145°43'E, coll. WFP, JW & F. Hermans, 8 February 1989 (AMw); Swansea (?), Tate coln., with *M. lacusedes* (SAM D19065d); Maria Island, W. Petterd coln. (AM C27755d); Hobart, W. Petterd coln. (AM C27754d).

Diagnosis. Umbones subcentral. Upper retractors of inhalant siphon relatively strong. Dorsal lobe of nephridium broad.

Shell. Rather large, usually 7–9 mm long (largest specimen measured: L 9.7 mm, H 8.5 mm, W/2 2.5 mm), somewhat elongated. Umbones almost central (Table 1). Mean density of internal pores 342±116 per mm^2 (n = 4). Siphonal retractors scars clear.

Anatomy. Siphons of living specimens (observed in sample from Blue Mountains) rather short, less than ½ of body length; inhalant and exhalant siphons equal in length and fused only at their base. Upper retractors of inhalant siphon relatively strong (in comparison to other subspecies). Up to eight embryos per pouch. Closed type of nephridium found in 14 of 20 studied specimens, otherwise small part of pericardial tube visible. Dorsal lobe of nephridium relatively broad.

Distribution (Fig. 56). From southern Queensland to Victoria, South Australia and Tasmania; more abundant in mountainous regions.

Ecology. Found in slow flowing creeks, swamps, lakes, waterholes and ponds.

Variability. As in the species in general, shell and some anatomical characters in this subspecies show a clear geographic pattern of variation. The forms represented in southern Queensland and northern NSW (correspond geographically and morphologically to *Sphaerium translucidum* Sowerby and *Sphaerinova nundialis* Iredale respectively) are rather similar in their large (up to 8.5 mm long) elongate and angulate shells with narrow and almost central umbones (Fig. 4A–E). Only the specimens from southern Queensland were anatomically studied, and they were characterised by an elongate dorsal lobe of the nephridium (Fig. 8A,B).

The form described as *Sphaerinova bradena* Iredale is distributed in eastern NSW (along the Great Divide and East coast); it is also large, but distinguished by its relatively high, rounded or angulate, compressed shell with a narrow umbo slightly shifted posteriorly (Figs. 3, 4F,G). The embryonic part of the shell in this form is relatively small. *Sphaerium macgillivrayi* E.A. Smith from the same area is smaller and its shell has central umbones. These differences may be due to individual variation.

A peculiar form inhabits the upper catchments of the Murray-Darling system; it is characterised by its smaller size (5.5 to 6 mm long), elongate, convex shell with central umbones, relatively broad embryonic shell and presence of faint sculpture (striation) (Fig. 4H–J). *Sphaerinova terenda* Iredale (Kuiper, 1983, fig. 8) and *S. victoriana* Iredale (Fig. 4I,J) are almost identical and represent this form. The shells from the lower Murray are similar to them but somewhat larger (Fig. 4K,L).

Most of the shells from Tasmania (the nominate form) are similar to the form from eastern NSW, but have somewhat broader umbones (Fig. 4M–O). An elongate symmetrical form with markedly protruding umbones (Fig. 4P) occurs in southeastern Tasmania (Hobart).

The lots of *Musculium tasmanicum tasmanicum* represented in available collections were not numerous, therefore it was not possible to carry out the statistical analyses needed to justify the status of the forms tentatively recognised here. After examination of additional materials, some of them may eventually be elevated to the status of subspecies, in addition to *M. tasmanicum queenslandicum*.

The number of embryos per brood pouch is also variable, but no geographical pattern was observed in the material studied.

Musculium (Sphaerinova) tasmanicum queenslandicum (E.A. Smith, 1883)

Fig. 9

Sphaerium queenslandicum E.A. Smith, 1883: 305, pl. 7, fig. 33; Iredale, 1943a: 196; Kuiper, 1983: 19 (in synonymy of *Sphaerium tasmanicum*).

Type material. HOLOTYPE BMNH 1879.5.21.779, Limestone Ck, Burdekin River, Qld.

Other material examined. QUEENSLAND: Rocky Ck, Atherton, coll. F. Allen (AM C313698d); East Baratha Ck, 14 miles north of Ayr, coll. Price, September 1958 (AMd); Little Brook, 5 km south of Proserpine on Bruce Hwy, coll. WFP, J. Burch & F. Colman, 30 April 1975 (AMd); Myke Ck, crossing no. 1 on Bruce Hwy, 5 miles north of Proserpine, coll. 4 May 1975 by WFP, F. Colman & J.B. Burch (AMd). NORTHERN TERRITORY: pool at mouth of canyon, Buffet Ck, south from Gulf of Carpentaria, 17°29'S 137°38'E, coll. WFP, J. Wilson & V. Kessner, 26 August 1991 (AMw).

Diagnosis. Umbones shifted posteriorly. Upper retractors of inhalant siphon weak. Dorsal lobe of nephridium narrow, elongated.

Shell. Rather small (maximum length 6.6 mm), relatively high. Umbones evidently shifted posteriorly (Table 1). Siphonal retractors scars weak, seen as small appendages of the posterior adductor scars.

Anatomy (only specimens from the Northern Territory studied). Upper retractors of inhalant siphon weak. Up to eight (usually four to six) embryos per pouch. Nephridia of closed type, dorsal lobe of nephridium elongate.

Distribution. Northern Queensland and Northern Territory (Fig. 56).

Ecology. As in nominate subspecies. Common in Queensland (on Atherton Tableland), rare in Northern Territory: only one population found despite extensive collecting in this region. According to W. Ponder (oral communication), high water temperature seems to be a principal factor limiting the distribution of these molluscs.

Variability and taxonomic remarks. The form observed here is distinguished from typical *M. tasmanicum* mainly by its peculiar shell outline and posteriorly shifted umbo. Differences in the LA/LP index that characterise the position of the umbo are statistically significant (values of index in Table 1, $t = 4.14$, $p<0.01$), but variation ranges overlap. Some differences in anatomical characters are also notable: the northern form has weaker siphonal retractors and an elongate dorsal lobe of the nephridia, but the range of variability in these characters is not known.

Both forms of *Musculium tasmanicum* are separated geographically. However, the nearest populations from northern and southern Queensland are morphologically the most similar. While the form observed here is morphologically distinct, the differences concern only a few characters.

One specimen from the Atherton Tableland, while having the characteristic shape of this subspecies, is distinguished by its rather solid shell and broader hinge plate. While no other specimens are currently available, the status of the form remains unclear.

Musculium (Sphaerinova) tatiarae (Cotton & Godfrey, 1938)

Figs. 10–14

Sphaerium tatiarae Cotton & Godfrey, 1938: 178, fig. 181; Iredale, 1943a: 195.
Sphaerinova bursa Cotton, 1953: 21.
Sphaerium tasmanicum Kuiper, 1983: 21, figs. 41, 42 (forms *tatiarae* and *bursa*).

Type material. HOLOTYPE SAM D12583, Tatiara Ck, Bordertown, SA. *Sphaerinova bursa*, holotype and paratype SAM D14453, River Torrens Lake, SA.

Other material examined. VICTORIA: Golden Ck, west of Corner Inlet, 38°45'S 146°10'E, coll. WFP, GC, R. de Keyzer & D. Beechey, 11 February 1990 (AMd); Spout Ck, 38°28'S 144°02'E, coll. FWA, 11 April 1988 (AMw); near gauge station on Mt Emu Ck, 38°19'S 142°53'E, coll. FWA, 23 April 1988 (AMw). SOUTH AUSTRALIA: Binnum Waterholes Police Paddock, Bordertown, coll. June 1886, Tomsett coln., with *M. tasmanicum* (SAM D19063d); Lake Torrens, Adelaide, coll. Major T. Cherry, with *Musculium* cf. *lacustre* (AM C42311d); Smiths Bay, Kangaroo Island, Cooper coln. (SAM D19067d); small swampy spring, east side of Lake Eliza, SE of Robe, 37°13'S 139°53'E, coll. WFP, 15 May 1984 (AMw); creek flowing in Lake George, north of Beachport, coll. IL & K. Handley, 27 February 1978 (AMw); Mt Gambier (AM C039180d). TASMANIA: Bowlers Lagoon, sample 1 in ti-tree area, coll. L. Mowra & T. Kingston, 23 September 1991 (QVM 9:12426w); Lagoon of Islands, coll. B.S. Mollison, 30 January 1965 (TMH E10977w); Rebecca Lagoon, coll. B.S. Mollison, 21 October 1963 (TMH E10980w); Lake Dulverton, coll. B.S. Mollison, October 1961 (TMH E10982d).

Material tentatively identified as *M. tatiarae*. NEW SOUTH WALES: Lake Binjie, south of Broken Hill, 33°18'S 141°48'E, 3–4 m above the current strand line, coll. J.W. Pickett, 1990 (AMd); Willow Dam, 25 miles from Griffith, 16 May 1972 (AMw). VICTORIA: Scotts Ck at Murfitt Rd Bridge, coll. FWA, 22 April 1988 (AMd); Darlot Ck, south of Ettric, 38°09'S 141°46'E, coll. A. Miller, 18 April 1994, with *P. aslini* (AM 302417d).

Diagnosis. Shell circular or short oval, solid, not transparent. Upper margin evenly curved, without angles. Umbones relatively broad, not protruding. Internal pores rare. Hinge plate broadened, cardinal teeth bent, lateral teeth normally developed.

Shell smaller than in *M. tasmanicum* (usually up to 6 mm long, some specimens 7–9 mm), circular or short oval, rather solid, white or yellow-coloured, not transparent. Dorsal margin evidently arched, merging to anterior and posterior ones without angles. Umbones of small specimens relatively broad and markedly shifted posteriorly, narrower (in relation to the whole shell) and centrally placed in larger specimens. Prodissoconch not

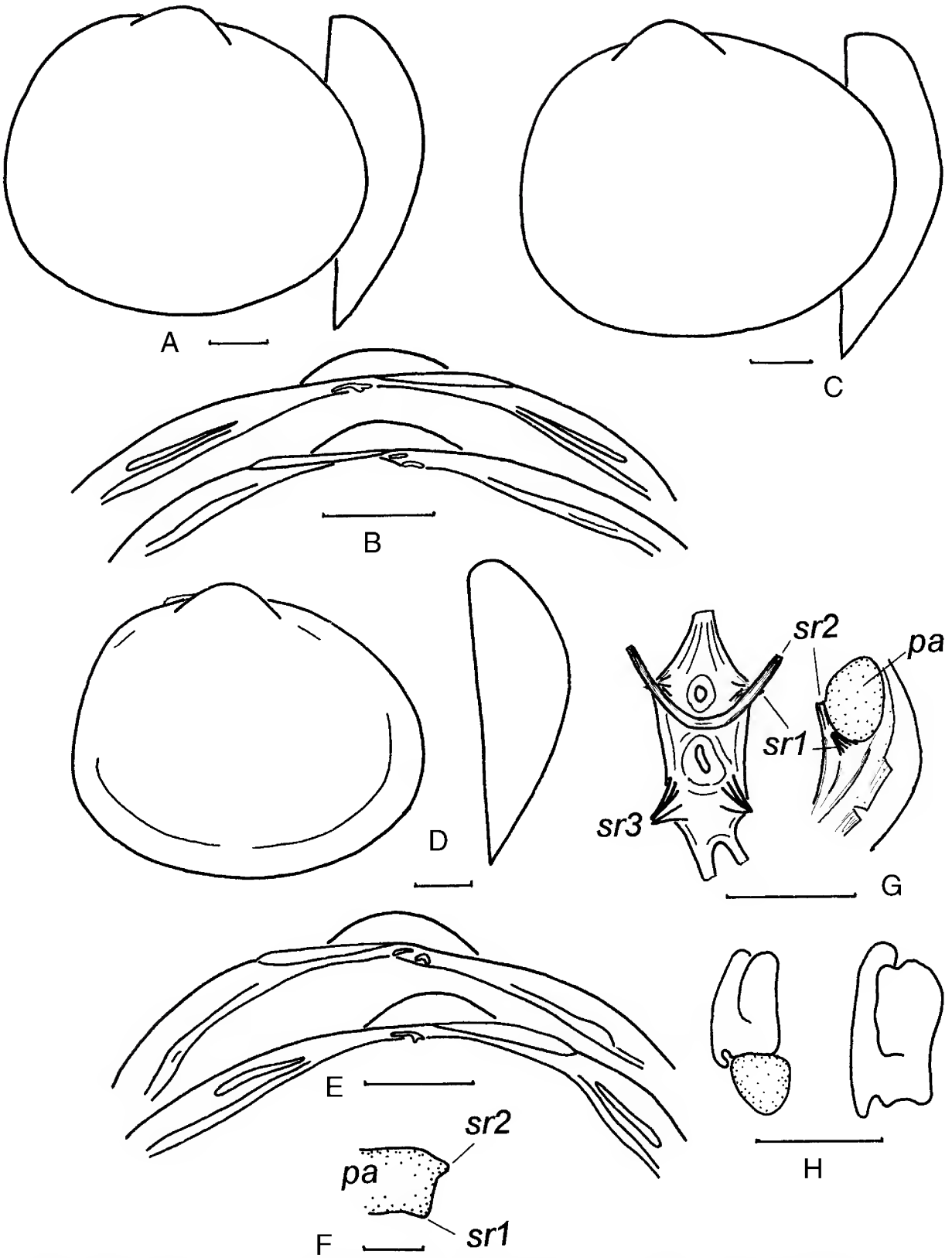


Figure 9. *Musculium tasmanicum queenslandicum* (E.A. Smith), shell and anatomy: A,B—north of Ayr, Qld (AM, no number), right valve and hinge; C—Atherton, Qld (AM C313698), right valve; D–H—Buffet Ck, NT (AM, no number), D—right valve, E—hinge, F—posterior muscle scars, G—siphons and siphonal retractors from inner side and left side, H—nephridia dorsally. Scale bars = 1 mm.

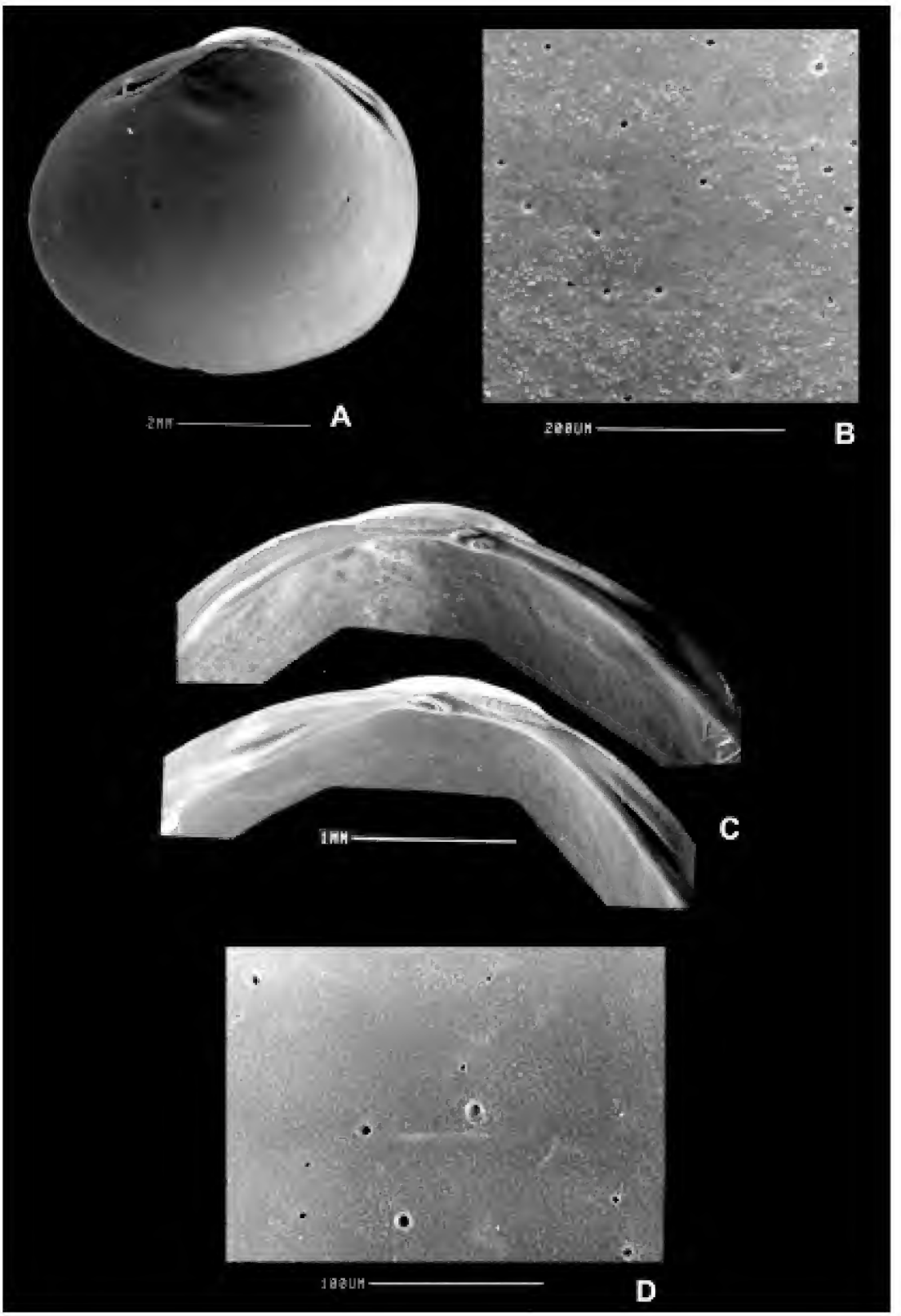


Figure 10. *Musculium tatiarae* (Cotton & Godfrey), shells: A—Bowlers Lagoon, Tas. (AM, no number), young specimen, right valve from inside; B—internal pores of the same specimen; C—Lake Eliza, SA (AM, no number), hinge; D—internal pores of this specimen.

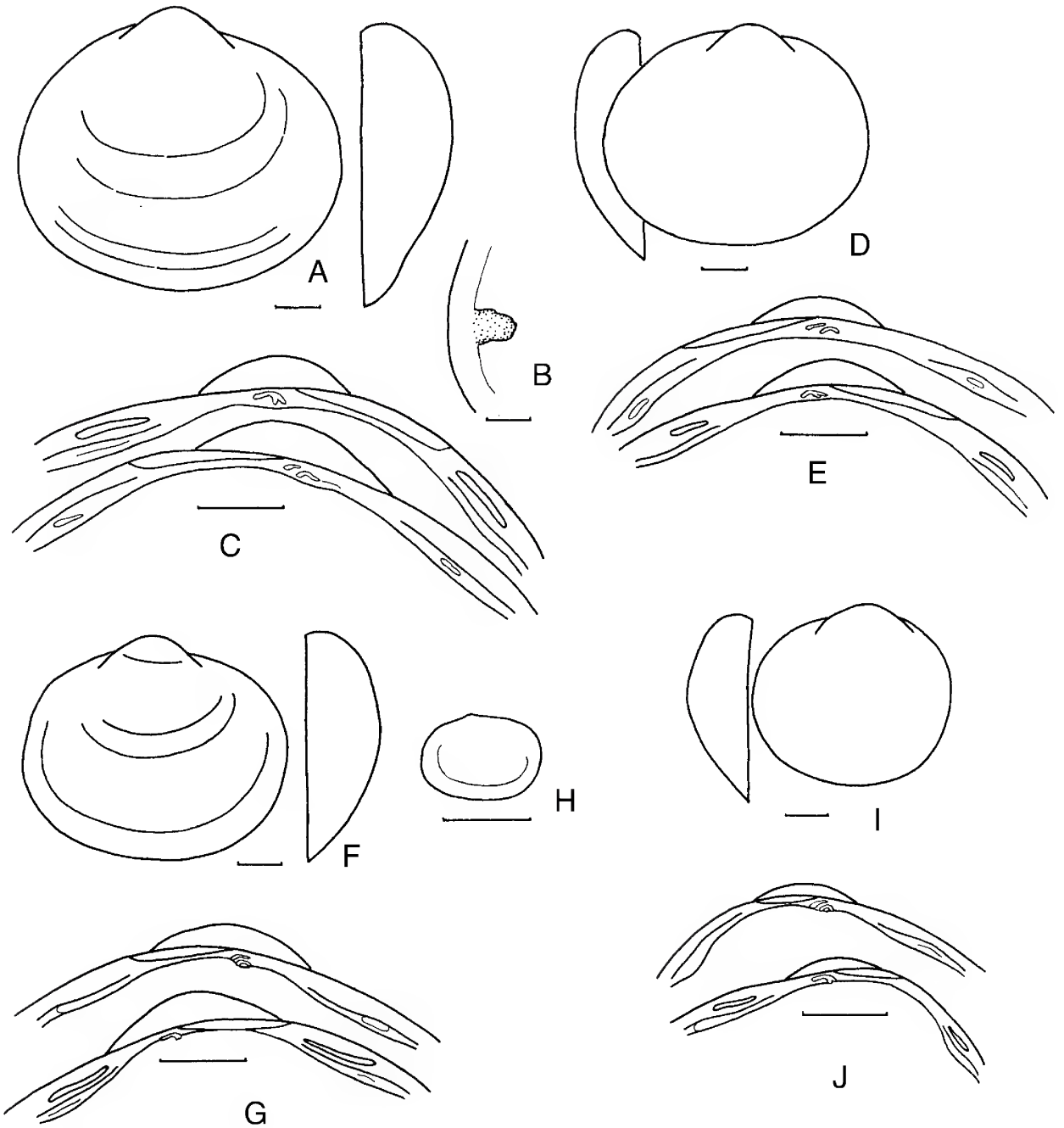
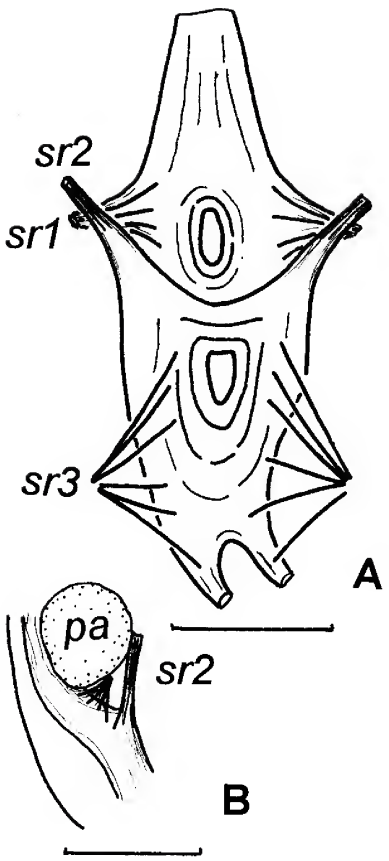


Figure 11. *Musculium tatiarae*, variation of shell form: A–C—holotype, Tatiarae Ck, SA (SAM D12583), A—right valve, B—posterior muscle scars, C—hinge; D,E—Binnum Waterhole, SA (SAM D19063), left valve and hinge; F–H—Bowlers Lagoon, Tas. (QVM 9:12426), F—right valve, G—hinge, H—young specimen; I–J—Lake Dulverton, Tas. (TMH E10982), left valve and hinge. Scale bars = 1 mm.

separated. Hinge plate relatively broad (Table 1). Surface smooth (sculpture not developed). Internal pores widely separated (density 157±62 per mm^2, n = 9). Scars of posterior adductors small, siphonal retractors scars merged to them. Ligament pit long, ligament exteriorly visible but usually not elevated. Cardinal teeth (c2 and c3) markedly bent or hooked, posterior end of c3 cleft. Lateral teeth evidently arched. Shells of young specimens elongate.

Anatomy. Characters of siphonal retractors and gills similar to those in *M. tasmanicum tasmanicum* (Figs. 12, 13). Three to four brood pouches per gill and up to seven embryos per pouch. Nephridium usually of open type (in 10 of 13 studied specimens), occasionally of closed type; dorsal lobe broad (Fig. 14).



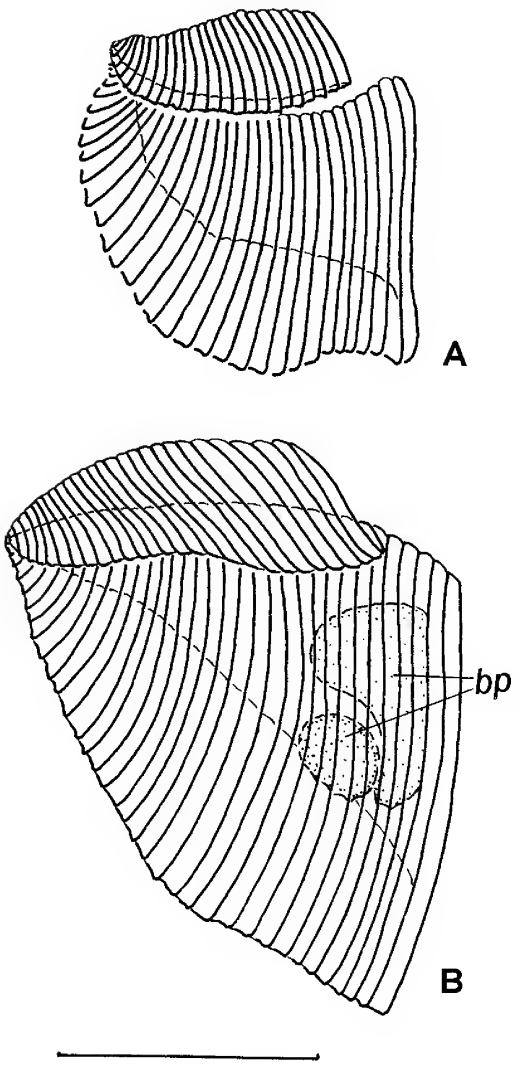


Figure 12. *Musculium tatiarae*, siphonal musculature, Bowlers Lagoon, Tas. (QVM 9:12426): A—from inside, B—from right side. Scale bars = 1 mm.

Figure 13. *Musculium tatiarae*, gills from outside: A—Lake Eliza, SA (AM, no number), young specimen; B—Lagoon of Islands, Tas. (TMH E10977), adult specimen. Scale bar = 1 mm.

Distribution. Southern Victoria, South Australia, northern Tasmania (Fig. 56). Specimens with similar characters occur in New South Wales, but their belonging to *M. tatiarae* needs confirmation.

Ecology. Most common in large lakes and lagoons. Occurs in smaller lakes, waterholes and creeks as well.

Variability. The largest shells (up to 9 mm long) are known from the area of Adelaide. Populations from the coastal lagoons of South Australia are characterised by smaller size (5 to 6 mm long), triangular or oval shell outline and posteriorly shifted umbo (Fig. 10C), as in the genus *Pisidium*. Tasmanian populations are intermediate in size and can be distinguished by circular outline and more centrally placed umbones (Figs. 10A, 11F–J).

The placement of the form from southern Victoria is not clear. It is similar to *M. tatiarae* in shell outline, shape and position of umbones (Fig. 21I–K). At the same time, it is distinguished by its narrow hinge plate, so the possibility that it may be a form of *M. tasmanicum* cannot be excluded. A very small, dwarf form was found in Darlot Ck (Fig. 21L). Some of the shells were only 3.5 mm long but contained 1–2 large embryos. The status of this form is also unclear.

Several specimens from the Murray-Darling system in New South Wales with thick shells and rather strong hinges (Fig. 21A–D) are also only tentatively identified as *M. tatiarae*.

Taxonomic remarks. The species can be distinguished from *M. tasmanicum* by the rounded shell outline, broad and posteriorly shifted umbo, broad and strongly curved hinge plate, hooked cardinal teeth and arched lateral teeth and

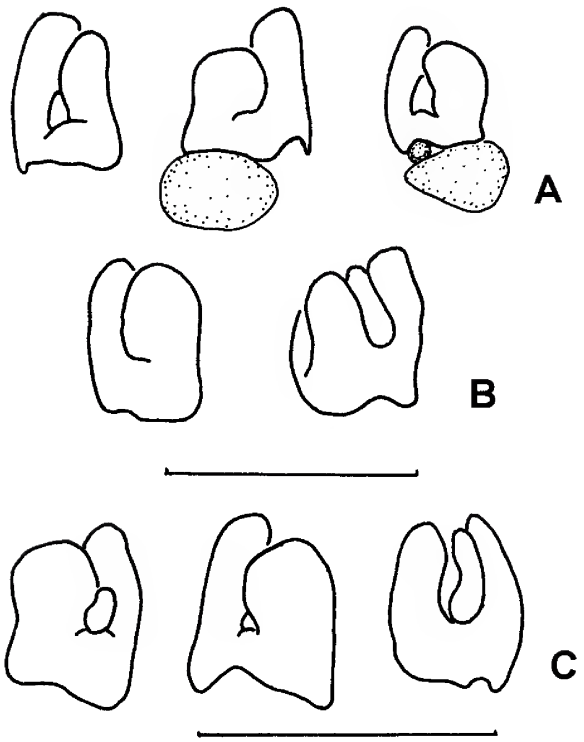


Figure 14. *Musculium tatiarae*, nephridia dorsally: A—Bowlers Lagoon, Tas. (QVM 9:12426); B—Lagoon of Islands, Tas. (TMH E10977); C—Lake Eliza, SA (AM, no number). Scale bars = 1 mm.

the widely spaced shell pores. Differences in the breadth of the hinge plate are statistically significant with $p<0.01$ (values of the index in Table 1, $t = 4.81$, $p<0.001$); the same concerns the differences in density of the internal pores ($t = 3.83$, $p<0.01$). The elongate outline of young shells is associated with the shape of the umbo (since the umbonal part of adult shell is formed in the early ontogenetic stages, the more elongate the young shell is, the broader the umbo will be). The white colour of the shell is also the distinctive character of *M. tatiarae*. Prevalence of the open nephridium type in *M. tatiarae* is also notable.

The differences in each of the characters described here are not large, but they agree well with each other. Applying several diagnostic characters, it is usually not hard to discriminate between *M. tasmanicum* and *M. tatiarae*. One lot containing both species without intermediates was found (Binnum Waterholes, Bordertown, see Figs. 9 and 23). Thus, the species distinctness of *M. tatiarae* is verified by sympatry and justified by several characters. At the same time, identification of specimens from Scotts Ck and Darlot Ck (Victoria) and Lake Binjie (southern New South Wales) as this species are tentative and require more material to determine their status.

Musculium (Sphaerinova) lacusedes (Iredale, 1943a)

Fig. 15

Sphaerinova lacusedes Iredale, 1943a: 195.
Sphaerium lacusedes.–Kuiper, 1983 (full synonymy).

Type material. Types not known, presumably they are lost, Great Lake, Tas.

Other material examined. TASMANIA: Great Lake, coll. Taffin, 2 June 1902 (TMH E5195d); Arthurs Lake, identified as *S. macgillivrayi* (SMF 87123d); South Esk River, W. Petterd coln. (AM C27756d); Swansea [sic, locality doubtful], Tate coln., with *M. tasmanicum* (SAM D19066d).

Diagnosis. Shell round or oval, thin but not transparent. Upper margin evenly curved, without angles. Umbones relatively broad. Internal pores dense. Hinge plate narrow, cardinal teeth curved, lateral teeth reduced.

Shell large (up to 9.5 mm long), round or oval, thin but not transparent, of yellowish colour. Anterodorsal margin straight, other margins merged to each other without angles, forming regular curve. Umbones central (median), prodissoconch not separated. Sculpture faint. Internal pores rather numerous, more than 400 per mm^2 (Kuiper, 1983). Hinge plate narrow. Cardinal teeth arched, c3 sometimes cleft. Lateral teeth evidently reduced, outer laterals in right valve absent. Ligament pit somewhat shorter than in *M. tasmanicum* (in relation to the shell length) (Table 1). Ligament visible from outside, elevated in large shells.

Anatomy known only from dried specimens. Dorsal retractor of inhalant siphon rather short and weak, as in *M. tasmanicum*; its scar usually merged with that of adductor, in a Frankfurt specimen (the largest one studied) it is well marked.

Distribution. Central Tasmania (Fig. 56).

Ecology. Mostly found in lakes, but at least one lot from the South Esk River is known. Apparently rare and is therefore a poorly studied species.

Taxonomic remarks. As mentioned by Kuiper (1983) and confirmed by the present study, reduction of the outer lateral teeth in the right valve is the most remarkable feature of *M. lacusedes*. This character seems to be constant. The yellowish colour of periostracum also seems to be diagnostic. However, the small number of available specimens is insufficient to reliably assess and data on morphological variability, and the data on the anatomy, distribution and ecology are still insufficient.

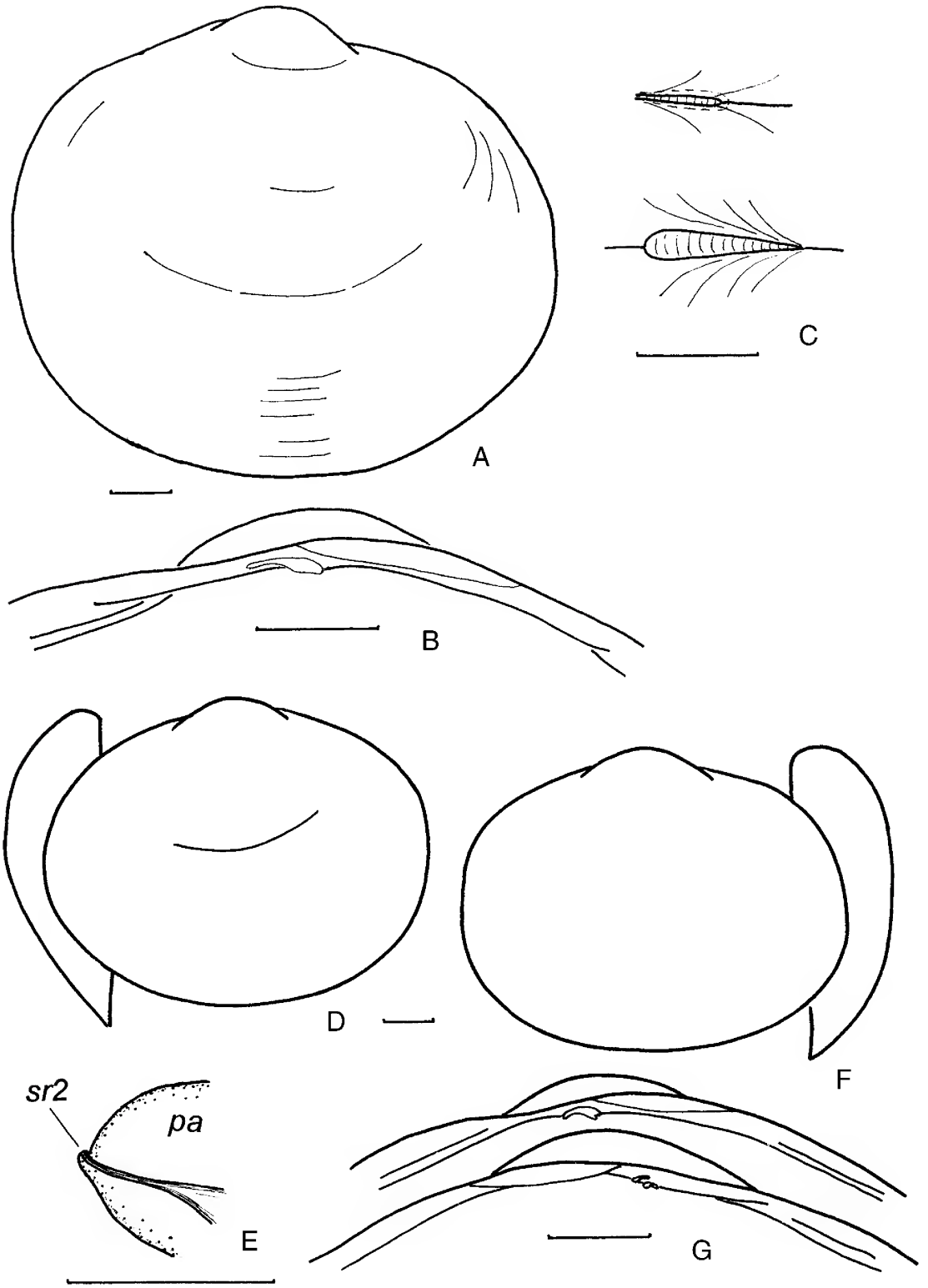


Figure 15. *Musculium lacusedes* (Iredale): A–C—Arthurs Lake, Tas. (SMF 87123), A—right valve, B—hinge of the right valve, C—ligaments of the young and the larger shell, from the dorsal side; D,E—Great Lake, Tas. (TMH E5195), D—left valve, E—dried muscles and their scars; F,G—South Esk River, Tas. (AM C27756), right valve and hinge. Scale bars = 1 mm.

Musculium (Sphaerinova) kendricki (Kuiper, 1983)

Fig. 16

Sphaerium kendricki Kuiper, 1983: 25, fig. 44–46.

Type material. HOLOTYPE WAM 649-74a, drain through Roselea nursery across North Beach Rd, Osborne Park, 31°54'S 115°50'E, WA. PARATYPES WAM 649-74b, 22 specimens, ZMA K-21018 to ZMA K-21023*, 6 specimens; same data as holotype.

Other material examined. WEST AUSTRALIA: drain from Herdsmans Lake, Perth, coll. G.P. Whitley, 27 December 1944, det. S.M. Slack-Smith (WAM 107/126-44d); Lake Monger, Lederville, coll. D. Edward, 23 November 1958, det. J. Kuiper (WAM 1053-66d); muddy lake near Jeloup turnoff, north of Capel, coll. J. Goodsell, 29 February 1976 (WAM 106-96d); Lake Nowergup 31°38'S 115°44'E, coll. F. Cheal & B. Robson, 9 November 1989, det. S.M. Slack-Smith (WAM 105-96w).

Diagnosis. Shell circular or short oval, solid, not transparent. Upper (dorsal) margin almost straight, with angles. Umbones broad, not protruding. Internal pores rare. Hinge plate broadened, cardinal teeth curved, lateral teeth normally developed.

Shell medium-sized (up to 8.2 mm long), circular or short oval, flat, rather solid, not transparent, of white colour. Dorsal margin long, slightly curved, with faint angles at anterior and posterior ends. Ventral margin evenly curved. Umbones central, relatively broad, not protruding, prodissoconch not separated. Sculpture: fine concentric striations. Scars of posterior adductors small, siphonal retractor scars merged to them. Internal pores rare. Hinge plate rather broad (Table 1). Ligament pit short and narrow, hinge relatively long. Ligament visible from exterior but not elevated. Cardinal teeth: c3 curved, deeply cleft on its posterior end, c2 curved or arched, c4 straight or slightly arched.

Anatomy. Siphonal retractors weak. Dorsal retractor of lower (inhalant) siphon short and weak. Outer demibranch relatively small. Two brood sacs and three generations of young, with one to five embryos each, found in single dissected specimen. Nephridium of closed type; lateral loop visible from outside.

Distribution. Southwestern Australia (Fig. 56).

Ecology. Lakes and lagoons.

Taxonomic remarks. Position of this species in the subgenus *Sphaerinova* is indicated by the following anatomical characters: nephridium with small excretory sac (generic character of *Musculium*), small outer demibranch, weak upper retractors of the lower siphon (subgeneric characters of *Sphaerinova*). It is distinguished from other Australian *Musculium* species by the peculiar shell outline, longer hinge (relatively large distance between the cusps of lateral teeth) and shorter ligament. The outline of the nephridium is also peculiar.

Musculium kendricki is similar to *M. tatiarae* in its solid shell, white colour and rather strong hinge teeth.

Musculium (Sphaerinova) quirindi n.sp.

Figs. 17–20

Sphaerium tasmanicum.–Kuiper, 1983: fig. 15.

Type material. HOLOTYPE AM C350024, shell dry, animal wet, Quipolly Ck, on Quirindi-Breeza Rd, NW of Quirindi, coll. WFP & AK, 19 September 1996. PARATYPES AM C350025d&w; 15 specimens, same data as holotype.

Other material examined. NEW SOUTH WALES: Attunga State Forest, 30°55'S 150°54'E, coll. IL & JW, 9 November 1985, with *M. tasmanicum* (AMw); Peel River, Tamworth, Musson coln. (AM C109829d); Kings Ck, tributary of McIntyre River, east of Inverell, 29°49'S 151°23'E (AM C109825d); Bell River, 19 km NW of Molong, coll. WFP and AK, 15 September 1996 (AM, 1 empty valve).

Diagnosis. Shell oval, solid, not transparent. Upper margin evenly curved, without angles. Umbones relatively broad, protruding. Internal pores dense. Hinge plate broadened, cardinal teeth arched, lateral teeth normally developed.

Shell medium-sized or small (Table 2), oval, rather inflated, solid and not transparent, white or yellowish. Holotype measurements: L 5.5, H 4.5, W/2 1.65 mm. Largest specimen measured: L 6.5, H 5.5, W/2 1.9 mm. Upper margin slightly curved, merging to anterior and posterior

Table 2. Measurements (mm) of paratypes of *Musculium quirindi* n.sp.

	L	H	HH	LL	LH	LA	LE	W/2
paratype	6.20	5.00	0.175	1.30	3.50	3.75	1.00	1.85
paratype	4.75	3.90	0.150	0.90	2.75	2.95	1.00	1.35
paratype	4.85	3.90	0.150	0.85	2.75	3.00	1.05	1.45
paratype	4.60	3.85	0.125	0.85	2.75	2.75	1.00	1.30
paratype	3.85	3.10	0.125	0.75	2.15	2.25	1.00	1.05

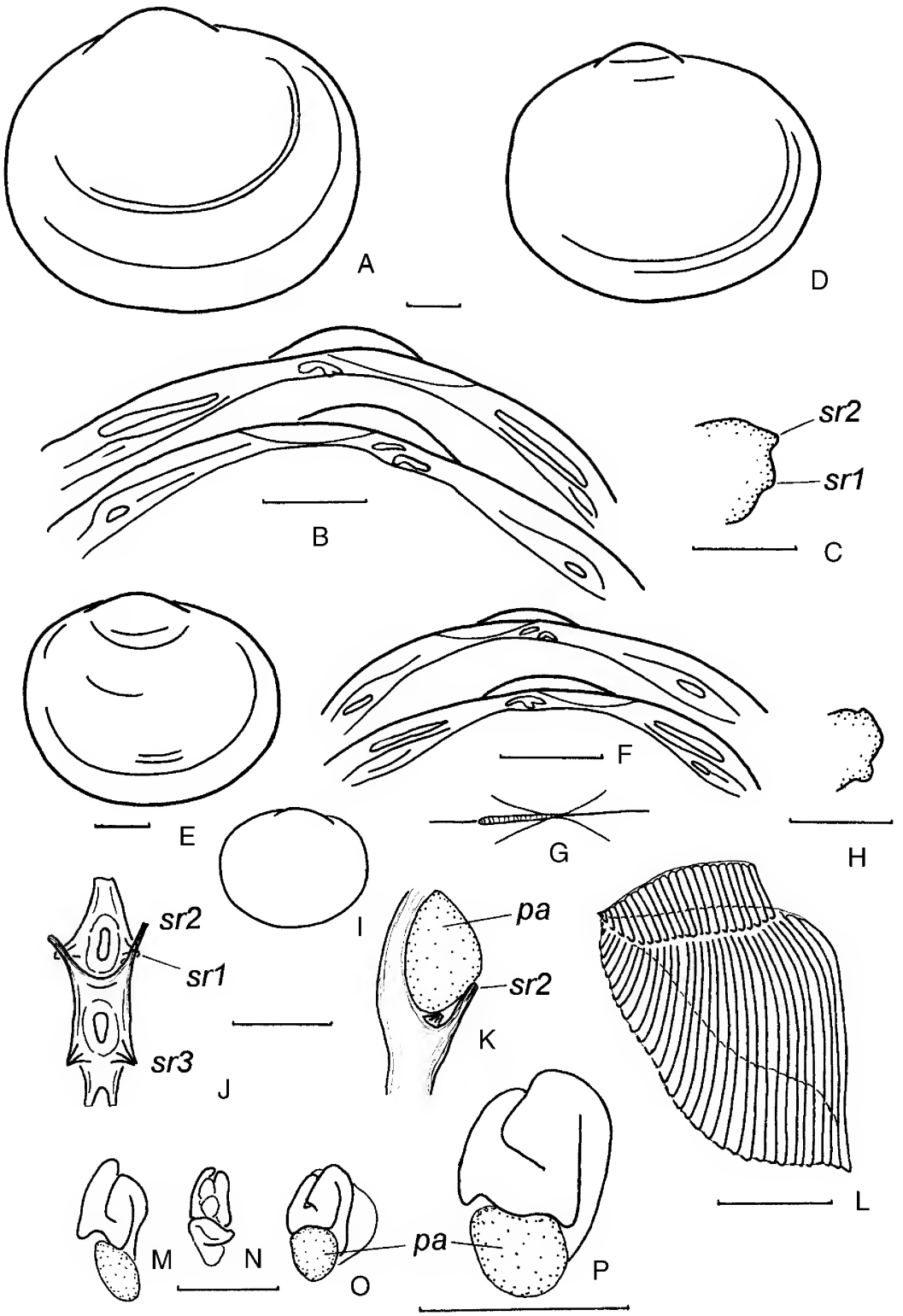


Figure 16. *Musculium kendricki* (Kuiper), shell and anatomy: A–C—Herdsmans Lake, WA (WAM 107/126-44), A—right valve, B—hinge, C—siphonal muscle scars; D—Lake Monger, WA (WAM 1053-66), elongated form, right valve; E–P—Lake Nowergup, WA (WAM 105-96), E—right valve, F—hinge, G—ligament dorsally, H—posterior muscle scars, I—shell of a young specimen, J—siphons and siphonal muscles from inside, K—the same, side view, L—gill from outside, M,O,P—nephridia dorsally, N—nephridium ventrally. Scale bars = 1 mm.

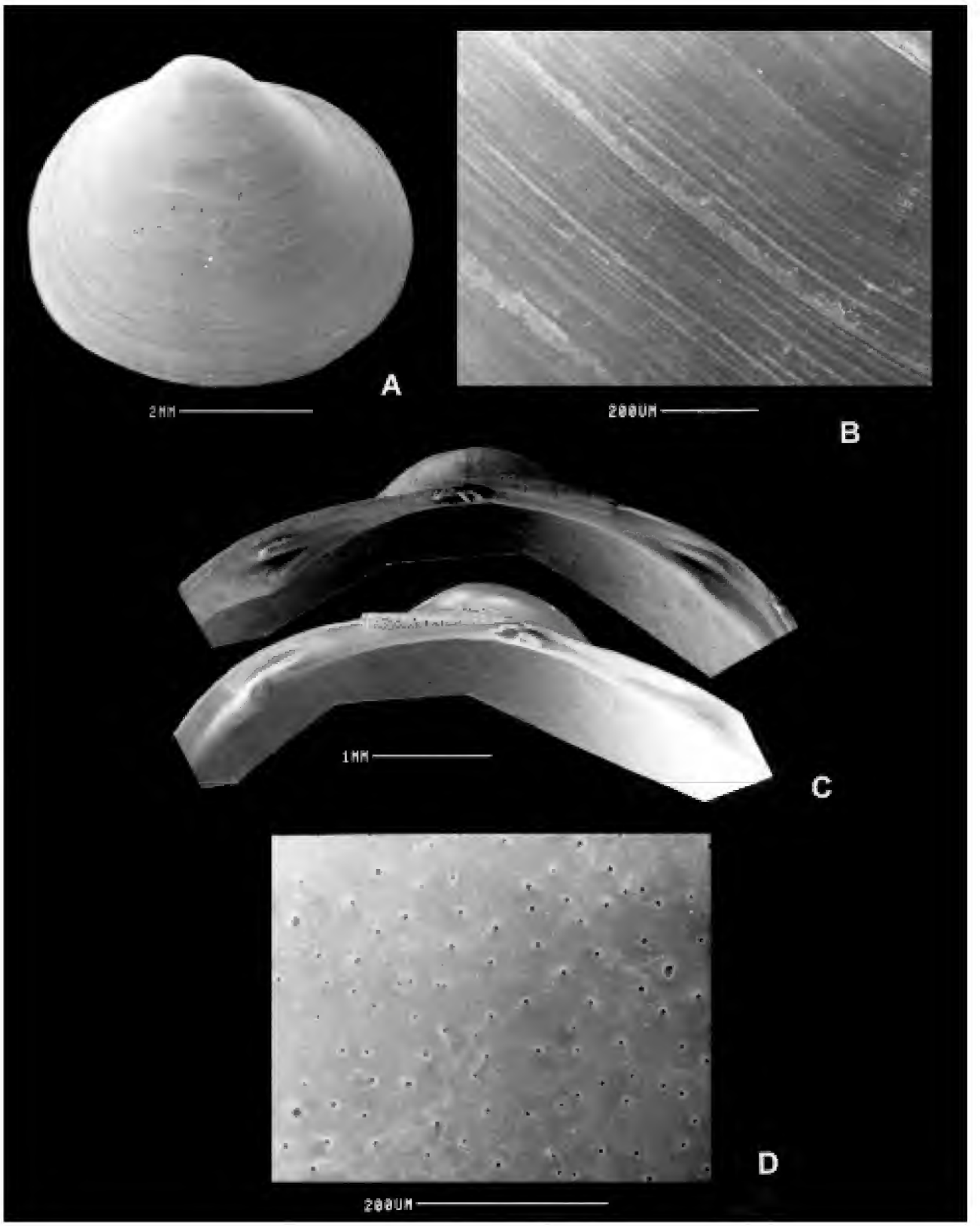


Figure 17. *Musculium quirindi* n.sp., type specimens, shells: A—right valve of the holotype (AM C350024) from outside, B—sculpture of the same specimen, C—hinge of the paratype (AM C350025), D—internal pores of the same specimen.

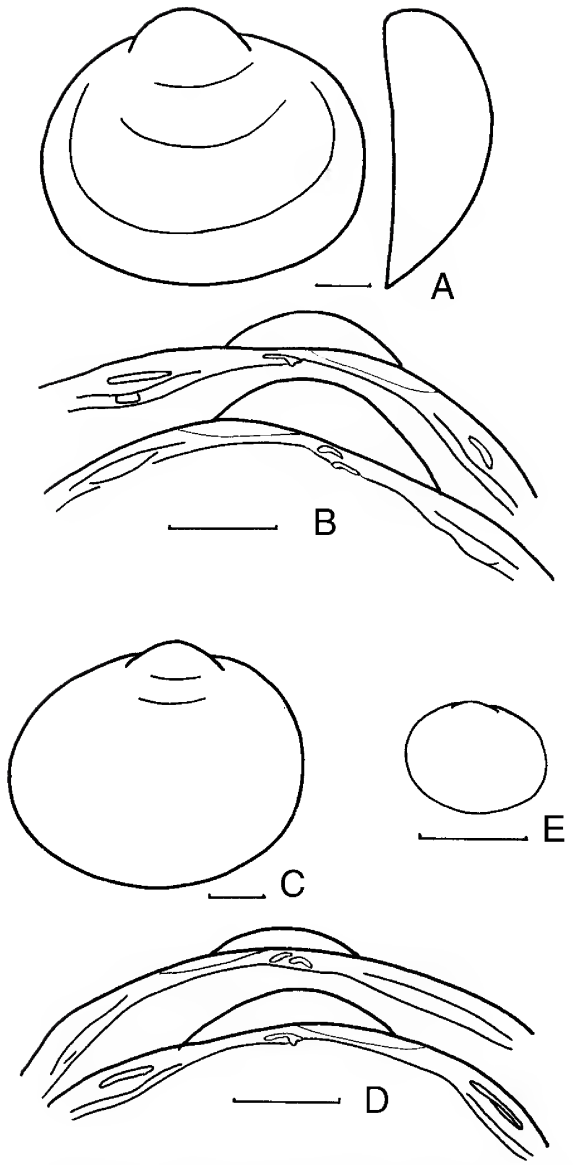


Figure 18. *Musculium quirindi*, variation of shell form: A,B—Attunga State Forest, NSW (AM, no number), right valve and hinge; C–E—Kings Ck (AM C109825), C—left valve, D—hinge, E—shell of a young specimen. Scale bars = 1 mm.

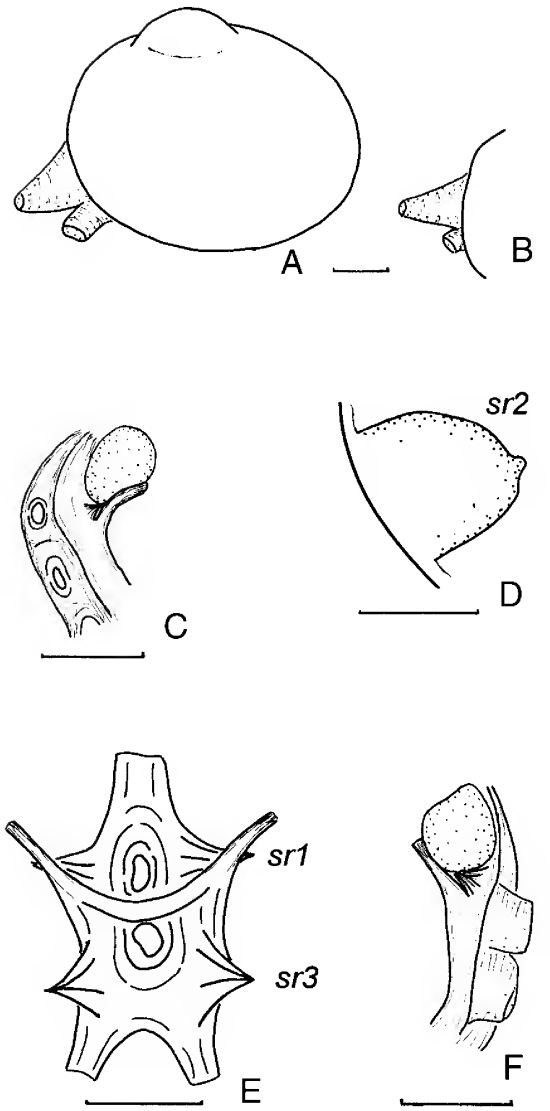


Figure 19. *Musculium quirindi*, siphons and siphonal musculature: A–E—paratypes (AM 350025); A,B—extended siphons of living specimens, C—siphonal muscles, side view, D—posterior muscle scars; F—Attunga State Forest, NSW (AM, no number), side view of siphons and siphonal muscles. Scale bars = 1 mm.

ones without angles. Posterior margin broad, truncated, anterior one narrow, somewhat elongate. Ventral margin slightly curved. Umbones submedian, in some specimens shifted posteriorly; protruded. Prodissoconch not separated. Internal pores numerous (643±35 per mm^2, n = 4). Scars of adductor muscles relatively large, those of siphonal retractors marked but not separated. Hinge plate relatively broad (Table 1, 2). Ligament pit long, ligament exteriorly visible but usually not elevated. Cardinal teeth arched, that of right valve cleft on its posterior end. Lateral teeth straight, thick, somewhat swollen. Young shells circular or short oval.

Anatomy. Upper (exhalant) siphon of living specimens markedly longer than lower one (only type lot observed, Fig. 19A–E). Dorsal retractors of inhalant siphon short but rather strong (in comparison with *M. tasmanicum*). Outer demibranch as in *M. tasmanicum*. Two to four brood pouches per gill with three to eight embryos each. Nephridia of open type, with short, broad dorsal lobe (Fig. 20).

Distribution. All studied lots are from the western slope of the Great Dividing Range, northeastern NSW (Fig. 56).

Ecology. Inhabits creeks, seems to prefer swift flow and thick vegetation.

Etymology. Named after the town nearest to the type locality—Quirindi.

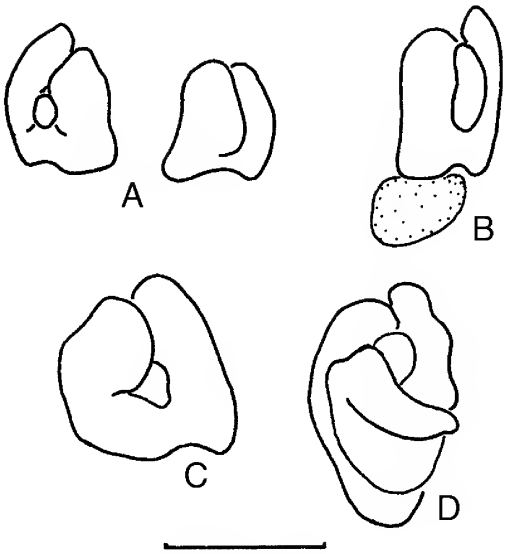


Figure 20. *Musculium quirindi*, nephridia: A,B—Attunga State Forest, NSW (AM, no number), dorsal view (two nephridia of one and the same specimen are figured in A); C,D—paratypes, dorsal and ventral views. Scale bars = 1 mm.

Variability and taxonomic remarks. Shell outline, position of umbo and hinge details are subject to individual variation. The new species is similar to the form of *M. tasmanicum* distributed in the upper Murray catchment but differs from it in its solid shell and strong hinge. These characters were also evident in the population from Attunga State forest living in sympatry with *M. tasmanicum*. The open type of nephridium (Fig. 20), rare in *M. tasmanicum*, is seen in this species. The new species is distinguished from *M. tatiarae* by its small, elongate and inflated shell as well as by its dense shell pores.

Musculium (?Sphaerinova) problematicum (Gabriel, 1939)

Fig. 21E–H

Sphaerium problematicum Gabriel, 1939: 128, pl. 4, fig. 36; Kuiper, 1983: 24, fig. 43 (full synonymy).

Type material. HOLOTYPE NMV F529*, Murray River, Merbein, Victoria. PARATYPES SAM D15675, 1 specimen; paratypes AM C63917, 2 specimens, NMV F584*, 21 specimens, same data as holotype.

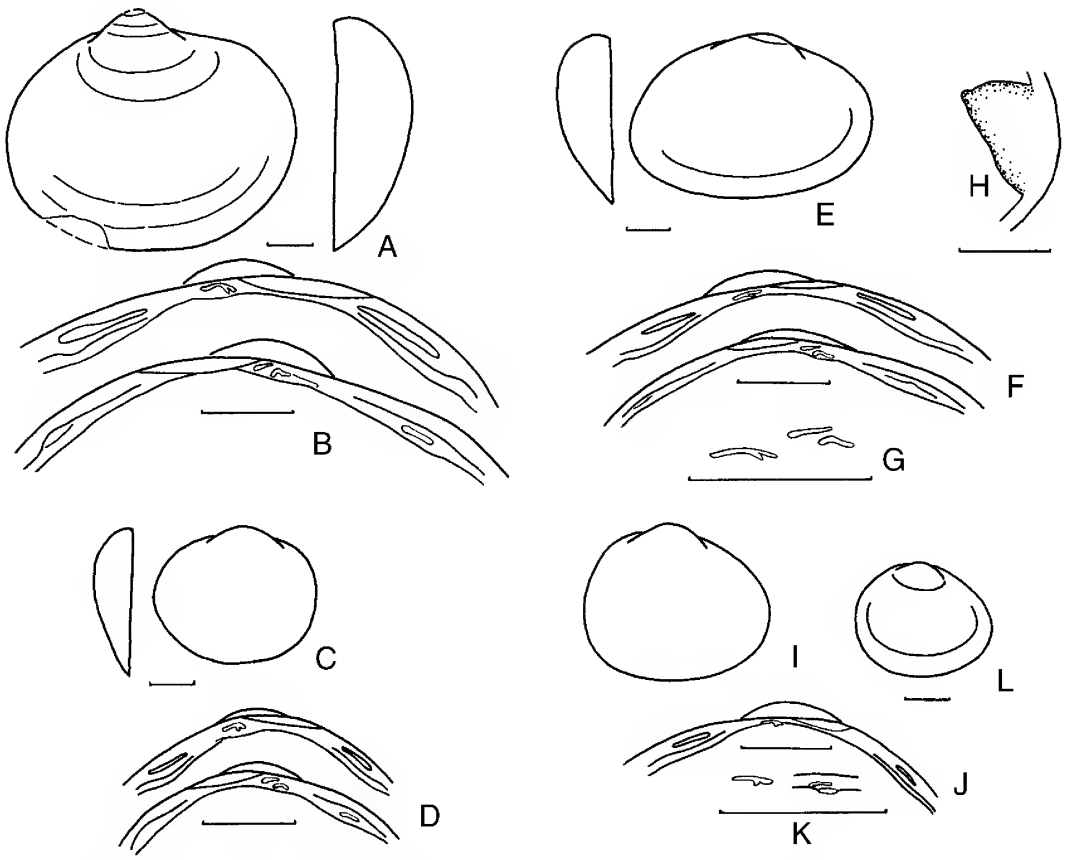


Figure 21. The forms of *Musculium* with undefined species status, shells: A,B—*Musculium* cf. *tatiarae*, near Griffith, NSW (AM, no number), right valve and hinge; C,D—*Musculium* cf. *tatiarae*, Lake Binjie, NSW (AM, no number), left valve and hinge; E–H—*M. problematicum* (Gabriel), paratype (AM C63917), E—right valve, F—hinge, G—cardinal teeth, H—posterior muscle scars; I–K—*Musculium* cf. *tatiarae*, Scotts Ck, Vic. (AM, no number), I—right valve, J—hinge of the right valve, K—cardinal teeth; L—*Musculium* cf. *tatiarae*, Darlot Ck, Vic. (AM C302417), right valve. Scale bars = 1 mm.

Only several lots from the type locality are available. These specimens differ from the other species by their elongate shell outline. However, they are similar to the species of *Sphaerinova* observed above in the shape of the muscle scars and ligament, and therefore the species may be tentatively included in that subgenus. Its status cannot be defined because of the scarcity of material and, given the variability of shell outline in species of *Musculium*, one cannot exclude the possibility that *M. problematicum* is just a local form of *M. tasmanicum*.

Subgenus *Musculium* s.str.

Type species. *Tellina lacustris* Müller, 1774, by monotypy.

Distribution. Europe, northern and eastern Asia, North America.

Diagnosis. Shell medium-sized (usually 8–10 mm long). Beaks median, definitely prosogyrous (bent anteriorly), protruded, with clearly separated prodissoconch usually forming a bean-shaped cap. Ligament not visible from exterior. Siphons long, dorsal retractors of branchial siphon normally developed, with their scars well marked as appendages of posterior adductor scars or separated.

Taxonomic remarks. Detailed characteristics of this subgenus are given in many reviews (Heard, 1977; Korniushin, 1996b). A short description of the type species and figures of a closely related or possibly conspecific taxon that is geographically nearest to Australia is provided below.

Musculium (Musculium) lacustre (Müller, 1774)

Figs. 22, 23

Sphaerium haasi C. Boettger, 1915 (SMF 1552w).

Material examined. Kiev, Ukraine, coll. AK, May 1997 (IZK); Dobo, Ins. Wammer, Aru, holotype of *Sphaerium haasi* C. Boettger, 1915 (SMF 1552w).

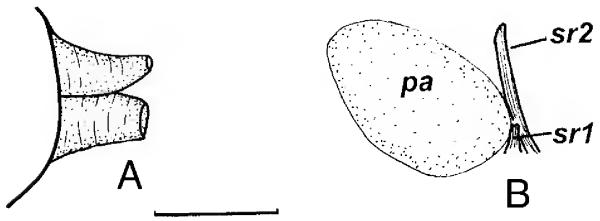


Figure 22. *Musculium lacustre* (Müll.), Kiev, Ukraine (collection of the author), siphons and siphonal muscles: A—extended siphons of the living specimen, B—posterior adductor and siphonal retractors, side view. Scale bar = 1 mm.

Diagnosis. Shell short oval, inflated, thin and fragile, transparent. Upper margin usually forming angles. Umbones median, with marked caps. Ligament not visible from exterior. Siphonal retractors strong, upper retractors of branchial siphon long. Nephridia usually of closed type.

Remarks. Very thin shell and marked caps of *Sphaerium haasi* (Fig. 23) evidently indicates that it belongs to the genus *Musculium* and has close affinity with *M. lacustre*. Presence of the latter species in Southeast Asia is suggested by recent reports (Morton, 1985). However, the forms from this region have some peculiarities in shell and anatomical characters and may represent closely related, but distinct species (Korniushin, in press). Extended discussion on this matter is beyond the scope of this paper.

Until now, *M. lacustre* or any other species of the nominate subgenus, were not recorded from Australia. In the course of this study, several specimens with large shells and strong siphonal retractors were found. They were so different from the common Australian *Sphaerinova* species, that their belonging to an introduced species of *Musculium* s.str., most probably to *M. lacustre*, is suggested.

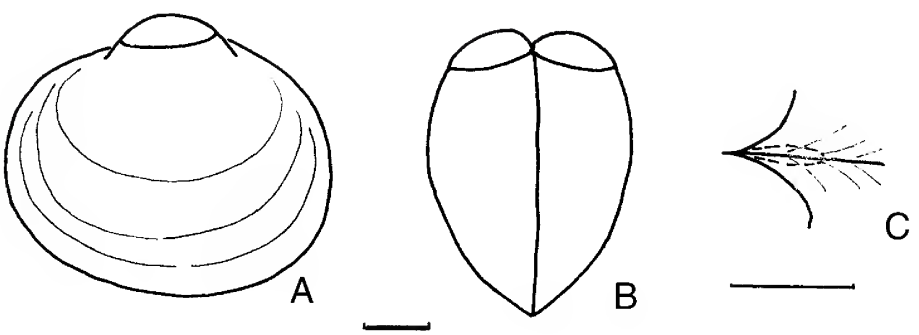


Figure 23. *Musculium lacustre*, Aru Islands (holotype of *Sphaerium haasi* C. Boettger, SMF 1552): A—lateral and B—anterior view of the shell, C—ligament dorsally. Scale bars = 1 mm.

Musculium (Musculium) cf. *lacustre* (Müller, 1774)

Fig. 24

Material examined. SOUTH AUSTRALIA: Lake Torrens, Adelaide, coll. Major T. Cherry, with *Musculium tatiarae* (AM C42311d, adult shell); Sturt River, Coromondel Valley, area of Adelaide (SAM D19068w, young specimens).

Shell large (length 11.5 mm, height 9.4, breadth 5 mm), rectangular, flat. Upper margin almost straight. Umbones narrow, shifted anteriorly and prosogyrous. Prodissoconch separated. Sculpture: fine striation and irregular folds. Hinge plate narrow, cardinal teeth: c2 short, triangular, c4 long, straight, c3 curved, not cleft. Lateral teeth long, posterior ones sharply bent, almost making right angle.

Anatomy. Only young specimens studied. Siphonal retractors strong, upper retractor of inhalant siphon long, attached to shell apart from posterior adductor. Three broods found in gills: free larvae and two brood pouches with two to four larvae in each. Nephridium of open type; dorsal lobe elongate.

Remarks. Identification of this very interesting form is tentative, because only one full-grown shell is available. This shell is similar to the large European forms of *M. lacustre*, particularly in the narrow protruding umbone and the separated prodissoconch (cap). The form from the Aru Islands assigned above to *M. lacustre* is much smaller. The specimens described

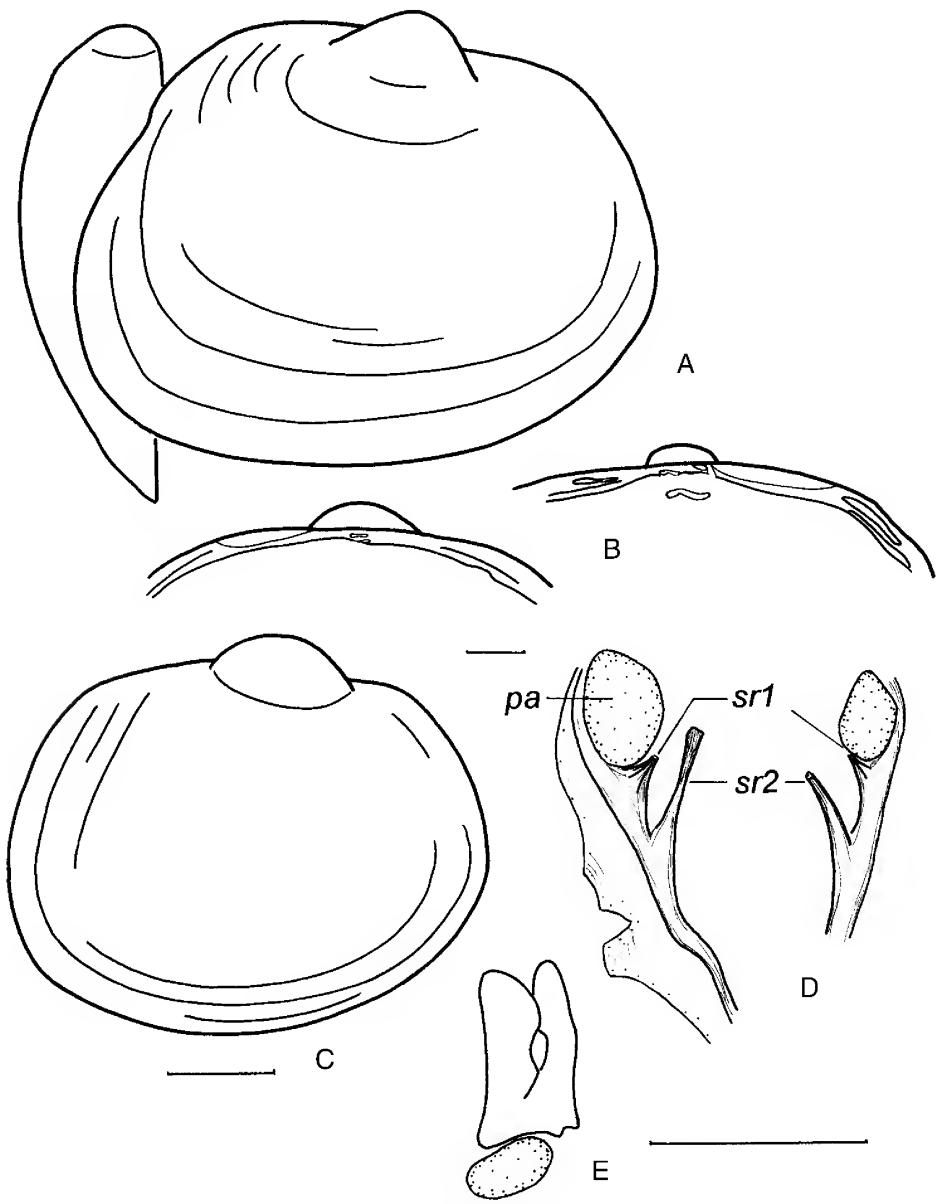


Figure 24. *Musculium* cf. *lacustre* (Müll.), shell and anatomy: A,B—Lake Torrens, Adelaide, SA (AM C42311), A—right valve, B—hinge; C–E—younger specimens from Sturt River, SA (SAM D19068), C—right valve, D—side view of posterior adductor and siphonal retractors, E—nephridium dorsally. Scale bars = 1 mm.

here show some similarity to the North American *M. transversum* (Say, 1829) in their straight upper margin and long lateral teeth, as well as in the long and strong upper retractors of the inhalant siphon, but the latter species has a much more elongated shell and broader umbone. Another similar species is known from the Amur River; it is included in the latest review of Palaearctic sphaeriids (Korniushin, 1996b) as *Paramusculium limanicum* (Moskvicheva, 1986), but further revision is necessary.

Musculium transversum was successfully introduced into England (Ellis, 1978). While both of the Australian localities of *Musculium* s.str. are situated near Adelaide, its introduction also seems probable. However, until more material is studied, the species cannot be identified with certainty and sources of introduction are not clear.

Incertae sedis

Cyclas egregia Gould, 1846

Cyclas egregia Gould 1846: 86.
Sphaerium egregium.–Kuiper, 1983: 24 (full synonymy)

Type material. Types not found, Hunter River, NSW.

None of the recent reviewers (Kuiper, 1983) cites the type specimens of this species. They are not listed in the malacological collection of the Museum of Comparative Zoology (Cambridge, Massachusetts), from which they were requested. In all probability, the types are lost. According to the original description (Gould, 1846), the species is characterised as very similar to *Sphaerium corneum* (Linneaus, 1758) but larger and with a more prominent ligament. The shell length should actually be about 20 mm (7/8 of an inch).

Sphaeriids with these characters have never otherwise been seen in Australia, and E.A. Smith (1883) doubted that original material was really Australian. However, it seems quite possible that Gould dealt with specimens of corbiculids, which are rather frequent in the large rivers (including the Hunter River). Specimens of juvenile *Corbicula* are quite often misidentified as sphaeriids.

Genus *Pisidium* Pfeiffer, 1821

Type species. *Tellina amnica* Müller, 1774 by subsequent designation (Gray, 1847).

Distribution. Cosmopolitan.

Diagnosis. Shell of medium size or small (usually up to 5 mm long, in some species 7–10 mm). Umbones placed posteriorly. Only exhalant siphon tubular; inhalant mantle opening without tubular extension or absent, only one pair of its retractors (ventral) present, other pair reduced. Outer demibranch with ascending lamella only (Korniushin, 1996b), or absent. Only one brood pouch in each gill. Nephridium with long funnel and small excretory sac without internal valve (Dreher-Mansur & Meier-Brook, 1992).

Remarks. The subgeneric division which is accepted by most reviewers after Kuiper (1962), is based on characters of gills, siphons and ligament. Subsequently, two major groups were distinguished by the type of brood pouch (Meier-Brook, 1970). New data encouraged some recent investigators (Adler, 1994; Korniushin, 1996b) to divide *Pisidium* into several genera. The number and composition of the new genera are, however, still controversial. Therefore, *Pisidium* is conservatively treated here as a single genus. The subgeneric divisions are based on those of Kuiper (1962), Zeissler (1971) and Burch (1975), with some nomenclatorial changes made below.

Subgenus *Afropisidium* Kuiper, 1962

Type species. *Pisidium lepus* Kuiper, 1957 = *P. pirothi* Jickeli, 1881 by original designation.

Distribution. South America, major part of Africa, south and Southeast Asia, Australia and New Zealand.

Diagnosis. Ligament external, elevated over dorsal margin. Only one (exhalant) siphon present; inhalant opening merged with pedal slit due to loss of presiphonal suture; ventral pair of siphonal retractors well developed, placed at posterior end of pedal slit. Outer demibranch absent. Brood pouch localised dorsally, formed by 7 to 20 filaments (depending on size of animal). Lateral loop of nephridium clearly visible from dorsal side.

Pisidium (Afropisidium) aslini Kuiper, 1983

Figs. 25–27

Pisidium aslini Kuiper, 1983: 35, fig. 65–69.

Type material. HOLOTYPE NMV F31522*, left bank at junction of Moleside Ck, Glenelg River, Vic. PARATYPES NMV F31533*, AM C135461, SAM*, WAM*, TMH E13349*, SMF 129900, about 200 specimens altogether, same data as holotype.

Other material examined. VICTORIA: Darlot Ck south of Ettric, 38°09'S 141°46'E, with *M. tatiarae* (?) (AM C302417d). TASMANIA: Greys Ck at Dunns Rd, SW of Smithton, 40°53'S 144°59'E, alt. 55 m, coll. WFP, JH & WP, 23 January 1982, with *P. tasmanicum* (AM C315738, from AM C135191w); Wandle River at Murchison Hwy, rock and gravel substrate, coll. WFP, JH & WP 23 January 1982, with *P. tasmanicum* (AM C135192w); tributary of Duck River, south of Roger River Township on Trowutta Rd, 41°00'S 145°03'E, coll. J. Clark & A. Miller, 8 February 1995 (AMw).

Diagnosis. Shell small compared to other species of the subgenus. Surface finely striated, sculpture more pronounced around umbo. Hinge plate narrow, cardinal teeth straight. Inner radial mantle muscles weak, forming six to eight bundles. Nephridia of the open type.

Shell very small (maximum 2.5 mm long), oval, moderately or strongly convex, thin, transparent or subtransparent. Margins evenly curved, without angles. Umbones rather broad, located in posterior 2/5 to 1/3 of shell length (Table 3). Sculpture: fine concentric striae, more pronounced around umbo. Pore density about 350 per mm^2. Mantle line usually poorly defined, mantle muscles scars elevated over mantle line but not separated from it. Hinge plate narrow, especially before and after cardinal teeth. Ligament pit short

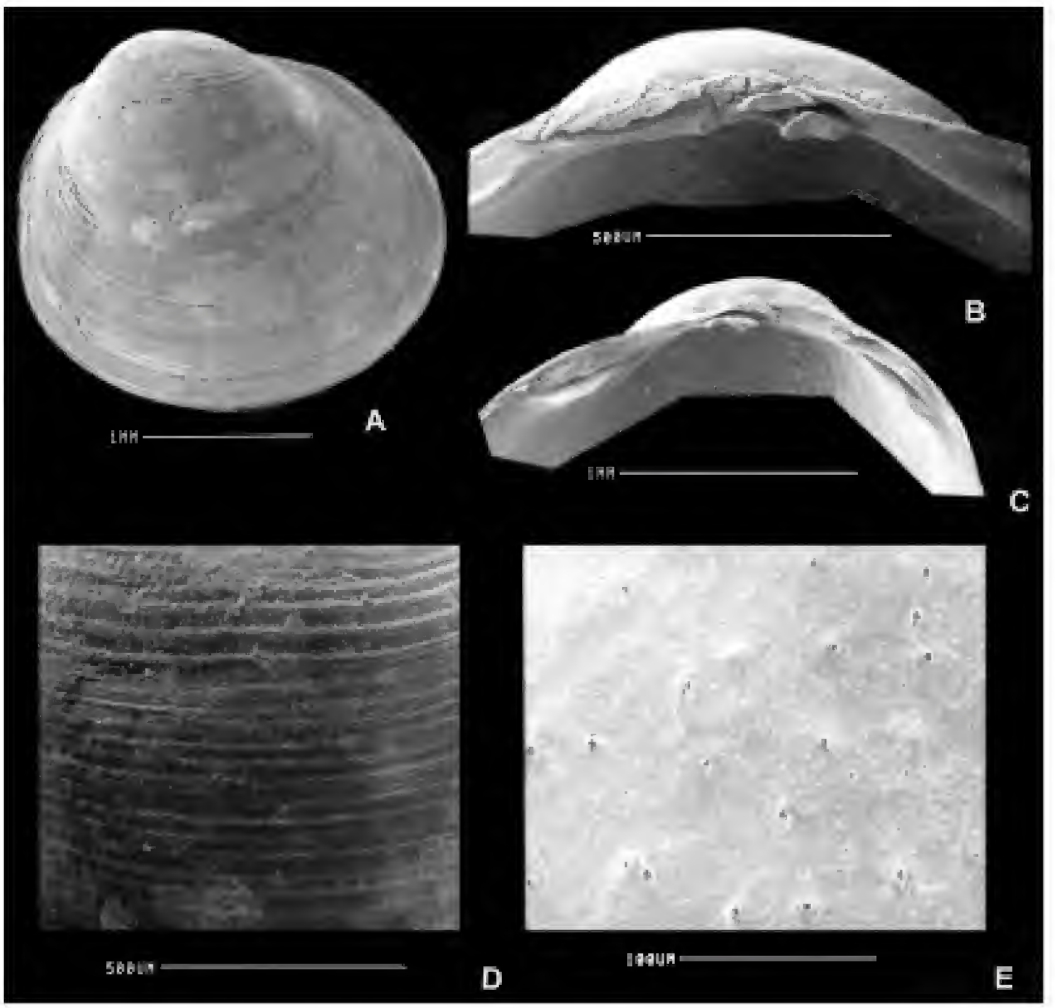


Figure 25. *Pisidium aslini* Kuiper, Wandle River, Tas. (AM C135192), shell: A—right valve from outside, B—hinge, C—sculpture, D—internal pores.

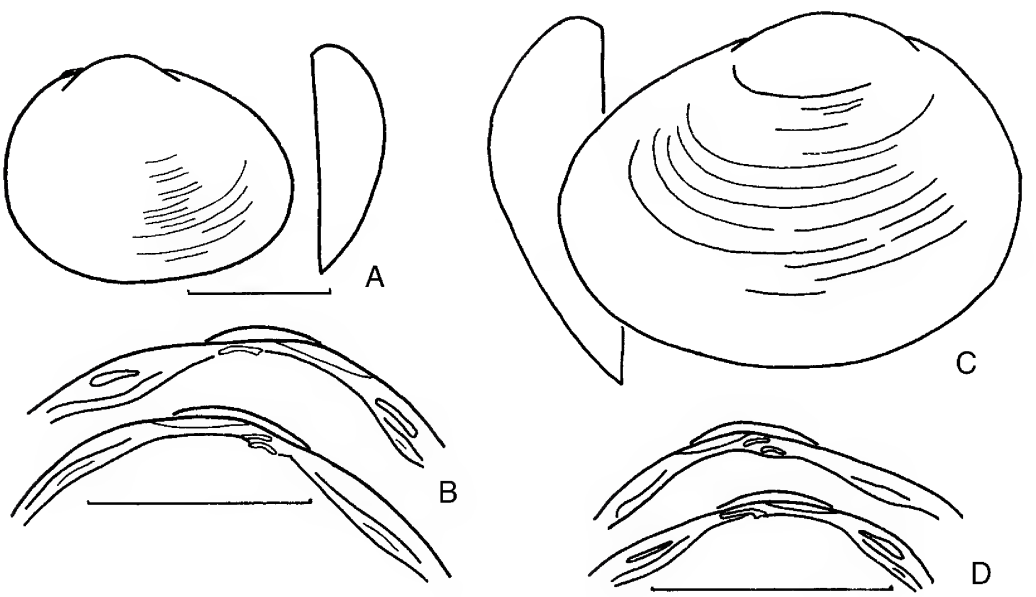


Figure 26. *Pisidium aslini* from Victoria, shells: A,B—paratype (AM C135461), right valve and hinge; C,D—Darlot Ck, Vic. (AM C302417), left valve and hinge. Scale bars = 1 mm.

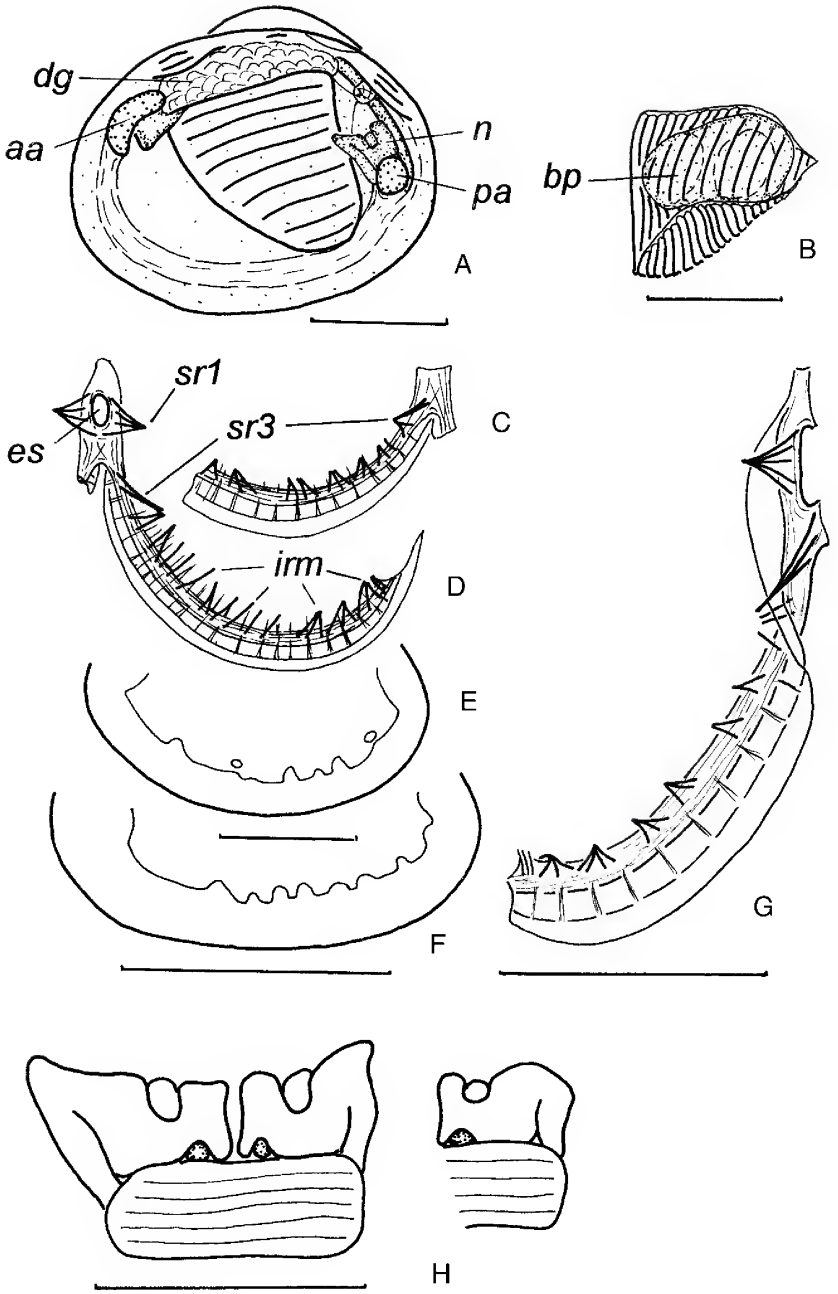


Figure 27. *Pisidium aslini*, Wandle River, Tas. (AM C135192), anatomy: A—gross anatomy; B—ctenidium with a brood pouch from inside; C,D,G—mantle muscles; E,F—mantle muscle scars; G—nephridia dorsally. Scale bars = 1 mm.

(Table 3), ligament markedly elevated. C2 in smaller specimens straight, in larger ones bent in middle, c4 straight, c3 slightly bent and thickened at posterior end. Lateral teeth moderately thick, rather short; a3 definitely shorter than a1, p1 and p3 of almost equal length.

Anatomy. Studied only in specimens from Greys Ck and Wandle River, Tas. Mantle edge rather narrow. Inner radial mantle muscles short (not much longer than outer radial muscles) and weak, six to eight bundles distinguishable.

Brood pouch placed dorsally and formed by seven filaments. Not more than two larvae found in each gill of gravid specimens.

Nephridia of open type with broad dorsal lobe, lateral loop clearly visible from dorsal side.

Distribution. While Kuiper (1983) mentioned only one locality—Glenelg River—this species is also known to occur in a few other localities in southern Victoria and northern Tasmania (Fig. 57C).

Table 3. Shell indices in the species of *Pisidium* (mean±SD, N - number of measured specimens, measurements shown in the Fig.1)

species and locality	N	H/L	HH/H	LL/L	LH/L	LA/LP	W/H
Pisidium aslini							
pooled, Tas.	9	0.82±0.022	0.054±0.007	0.20±0.013	0.57±0.026	1.45±0.165	0.74±0.049
pooled, range		0.77–0.84	0.044–0.063	0.18–0.21	0.54–0.63	1.24–1.72	0.66–0.80
Pisidium australiense							
pooled	6	0.86±0.018	0.046±0.011	0.13±0.015	0.57±0.014	1.36±0.058	0.70±0.047
pooled, range		0.85–0.90	0.032–0.065	0.12–0.17	0.55–0.59	1.31–1.47	0.67–0.79
Pisidium etheridgei							
northern NSW	4	0.83±0.006	0.041±0.018	0.21±0.014	0.50±0.030	1.28±0.106	0.67±0.057
Mt. Kaputar, NSW	10	0.81±0.019	0.049±0.010	0.22±0.015	0.52±0.038	1.22±0.616	0.63±0.040
Bobundara Ck, NSW	12	0.81±0.015	0.045±0.008	0.19±0.015	0.51±0.028	1.29±0.062	0.58±0.048
Alpine Ck, NSW	3	0.84±0.005	0.038±0.007	0.20±0.009	0.47±0.028	1.23±0.148	0.64±0.032
Morwell Rv trib., Vic.	5	0.84±0.019	0.042±0.002	0.23±0.013	0.53±0.025	1.33±0.095	0.67±0.038
Chinaman's Ck, Vic.	20	0.83±0.013	0.058±0.007	0.23±0.019	0.57±0.015	1.15±0.077	0.62±0.030
Urquart Ck, Tas.	3	0.83±0.018	0.055±0.012	0.21±0.008	0.53±0.003	1.28±0.072	0.65±0.081
Lake Butters, Tas.	14	0.81±0.017	0.039±0.007	0.17±0.022	0.52±0.016	1.23±0.072	0.54±0.048
Lake Sorell, Tas.	5	0.81±0.015	0.050±0.014	0.20±0.011	0.51±0.012	1.30±0.090	0.63±0.043
pooled	76	0.82±0.020	0.048±0.010	0.21±0.048	0.53±0.035	1.24±0.096	0.61±0.065
pooled, range		0.77–0.86	0.020–0.074	0.14–0.28	0.45–0.62	0.99–1.43	0.47–0.74
Pisidium hallae							
Barrington Tops, NSW	20	0.78±0.016	0.046±0.009	0.22±0.020	0.51±0.014	1.25±0.062	0.58±0.032
Blue Mountains, NSW	12	0.77±0.016	0.057±0.008	0.21±0.012	0.51±0.016	1.25±0.093	0.67±0.034
Warburton, Vic.	5	0.77±0.008	0.047±0.001	0.22±0.012	0.48±0.028	1.28±0.079	0.66±0.040
Ben Lomond Rv, Tas.	5	0.79±0.007	0.046±0.011	0.20±0.018	0.51±0.031	1.41±0.113	0.64±0.010
Franklin Rv, Tas.	7	0.77±0.013	0.051±0.006	0.21±0.011	0.49±0.024	1.34±0.079	0.67±0.041
pooled	49	0.78±0.015	0.050±0.009	0.21±0.016	0.50±0.022	1.29±0.092	0.63±0.055
pooled, range		0.73–0.82	0.026–0.071	0.18–0.27	0.46–0.55	1.15–1.54	0.52–0.74
Pisidium kosciusko							
Lake Albino, NSW	13	0.81±0.021	0.037±0.011	0.19±0.017	0.53±0.027	1.21±0.074	0.61±0.054
range		0.79–0.86	0.016–0.054	0.17–0.22	0.49–0.58	1.04–1.34	0.49–0.68
Pisidium tasmanicum							
Morwell Rv trib. Vic.	18	0.84±0.025	0.050±0.009	0.20±0.024	0.51±016	1.34±0.140	0.70±0.045
Deep Ck, Vic.	10	0.82±0.009	0.051±0.009	0.18±0.011	0.52±0.016	1.36±0.079	0.64±0.039
Frasers Ck, Vic.	7	0.84±0.014	0.046±0.007	0.21±0.016	0.55±0.021	1.22±0.128	0.63±0.034
Nora Rv, Tas.	4	0.85±0.018	0.051±0.005	0.26±0.029	0.52±0.031	1.13±0.038	0.71±0.023
Wandle Rv, Tas.	10	0.83±0.018	0.052±0.010	0.19±0.013	0.56±0.025	1.28±0.118	0.71±0.034
type lot? Tas.	3	0.82±0.004	0.050±0.015	0.19±0.010	0.53±0.003	1.30±0.059	0.64±0.034
Lake Dulverton, Tas.	4	0.85±0.016	0.046±0.011	0.18±0.010	0.52±0.014	1.35±0.151	0.54±0.293
Ben Lomond Rv, Tas.	3	0.86±0.013	0.042±0.004	0.16±0.008	0.51±0.022	1.31±0.110	0.66±0.026
pooled	58	0.84±0.018	0.050±0.009	0.20±0.026	0.53±0.026	1.31±0.120	0.68±0.048
pooled, range		0.80–0.90	0.033–0.071	0.15–0.33	0.48–0.60	1.05–1.60	0.57–0.77
Pisidium fultoni							
Lake Butters, Tas.	13	0.83±0.015	0.043±0.005	0.21±0.014	0.56±0.021	1.26±0.093	0.56±0.032
Lake Malbena, Tas.	10	0.83±0.020	0.044±0.011	0.21±0.019	0.58±0.033	1.23±0.077	0.56±0.023
pooled	23	0.84±0.018	0.043±0.011	0.21±0.016	0.57±0.027	1.25±0.087	0.56±0.028
pooled, range		0.80–0.86	0.031–0.064	0.19–0.24	0.51–0.62	1.09–1.48	0.52–0.63
Pisidium carum							
Gympie, Qld	6	0.82±0.006	0.061±0.004	0.18±0.018	0.56±0.038	1.12±0.039	0.61±0.041
Caboolture, Qld	6	0.81±0.019	0.065±0.005	0.19±0.016	0.54±0.036	1.13±0.57	0.60±0.035
Molong Ck, NSW	9	0.83±0.014	0.067±0.009	0.19±0.019	0.55±0.020	1.10±0.067	0.63±0.037
Carnarvon, NSW	4	0.81±0.006	0.055±0.004	0.18±0.016	0.57±0.024	0.97±0.018	0.58±0.008
Loddon Rv, Vic.	20	0.83±0.012	0.056±0.006	0.19±0.017	0.56±0.031	1.11±0.054	0.60±0.036
pooled	45	0.82±0.015	0.060±0.008	0.19±0.018	0.56±0.030	1.10±0.066	0.60±0.037
pooled, range		0.79–0.86	0.042–0.081	0.16–0.24	0.47–0.61	0.95–1.28	0.54–0.71

Table 3. Continued.

species and locality	N	H/L	HH/H	LL/L	LH/L	LA/LP	W/H
Pisidium ponderi							
Bindi Brook, NSW	5	0.82±0.009	0.052±0.010	0.21±0.027	0.53±0.016	1.13±0.027	0.65±0.046
Tia Rv, NSW	10	0.84±0.009	0.047±0.007	0.21±0.014	0.56±0.027	1.13±0.050	0.67±0.030
type lot, NSW	11	0.83±0.017	0.052±0.009	0.21±0.021	0.55±0.010	1.28±0.146	0.73±0.070
pooled	26	0.83±0.029	0.050±0.009	0.21±0.019	0.55±0.021	1.20±0.127	0.70±0.060
pooled, range		0.80–0.86	0.037–0.073	0.17–0.25	0.50–0.58	1.04–1.54	0.60–0.87
Pisidium centrale							
pooled	8	0.81±0.011	0.056±0.014	0.19±0.016	0.57±0.015	1.07±0.063	0.56±0.039
range		0.79–0.83	0.034–0.078	0.17–0.22	0.56–0.60	1.00–1.17	0.49–0.60

Ecology. Inhabits creeks, is often associated with *P. tasmanicum*, in Darlot Ck it is found together with *Musculium tatiarae*.

Variability. The form from Tasmania (Fig. 25) has definitely higher and more inflated shells with weaker sculpture than the typical form (Fig. 26).

Taxonomic remarks. The placement of *Pisidium aslini* in the subgenus *Afropisidium* is based on there being an externally visible ligament (Kuiper, 1983). Principal anatomical characters (absence of inhalant mantle opening and outer demibranch, upper position of brood pouch, dorsally visible lateral loop of nephridium) are shared by two other subgenera, namely *Neopisidium* Odhner and *Odhneripisidium* Kuiper.

In shell characters, *Pisidium aslini* differs from the other species of *Afropisidium* by its smaller size, being similar to the smallest species of *Neopisidium* and *Odhneripisidium*. It is also characterised by the extreme reduction of mantle musculature and peculiar configuration of the nephridium: while in the other *Afropisidium* species the lateral loop is bent (with some portion lying transversely) and the dorsal view of nephridium is S-shaped, in *P. aslini* the lateral loop is almost straight, stretching parallel to the body axis (Fig. 27G).

The Tasmanian form of *P. aslini*—on which the anatomical description is based—differs from the typical Victorian one in its more convex shell, somewhat protruding umbo and less-pronounced sculpture, and may represent a distinct subspecies or even a species. However, more material is needed in order to define its status.

Subgenus *Odhneripisidium* Kuiper, 1962

Type species. *Pisidium stewarti* Preston, 1909 by original designation.

Distribution. Central and southern part of Eurasia, Sunda Archipelago, northern Australia, occasionally in North Africa, and (probably) in Papua New Guinea (Kuiper, 1983).

Diagnosis. Ligament introverted (Kuiper, 1962), stretching toward ventral side of hinge plate. Anatomical characters as in *Afropisidium*.

Pisidium (Odhneripisidium) australiense n.sp.

Figs. 28, 29

Type material. HOLOTYPE AM C350022d&w, gold coated for SEM, Dowah Ck upstream from the junction with Freshwater Ck, Crystal Cascades, W of Cairns, 16°58'S 145°41'E, Qld, in quiet corners of swift creek, coll. WFP, 30 September 1980. PARATYPES AM C350023w, 6 specimens, one valve gold coated for SEM, same data as holotype.

Other material examined. QUEENSLAND: Broomfield Ck at Innisfail-Japoon Rd, 17°44'S 145°56'E, small boulders and gravel, coll. WFP, 28 September 1980 (AMw&d); Douglas Ck at Palm Hwy west of Cairns, on stones and leaves in pools, coll. WFP, 28 September 1980 (AMw&d); Dowah Ck, coll. WFP, 30 September 1980 (AMw&d).

Diagnosis. Shell small, with fine broad-spaced ribs. Hinge plate narrow, cardinal teeth curved. Inner radial mantle muscles weak, about five bundles are clearly distinguishable. Nephridia of closed type.

Shell very small (Table 4, largest specimen examined: 2.17 mm long), tetragonal, rather flat, thin, sub-transparent. Upper margin straight, with more-or-less clear angles at its extremities, front margin oblique, curved on its low extremity, ventral margin slightly

Table 4. Measurements (mm) of *Pisidium (Odhneripisidium) australiense* n.sp.

	L	H	HH	LL	LH	LA	W/2
holotype	2.17	1.86	0.059	0.29	1.20	1.31	0.74
paratype	2.08	1.87	0.088	0.25	1.22	1.19	0.62
paratype	2.03	1.75	0.071	0.27	1.20	1.16	0.62
paratype	1.85	1.57	0.067	0.27	1.08	1.06	0.57
paratype	1.75	1.49	0.097	0.29	0.99	1.01	0.52

curved, back margin truncate. Umbones at posterior 2/5 of shell length (Table 3), narrow, flat (not protruded). Sculpture: fine but clear broad-spaced concentric ribs. Internal pores numerous: 861 per mm^2 (one measurement). Mantle line and adductor scars clear, several mantle muscles scars elevated over mantle line but not separated from it. Hinge plate narrow near ligament, broadened around cardinal teeth. Ligament pit triangular, somewhat elongate in comparison with other species of subgenus. Cardinal teeth: c2 strongly curved, triangular, c4 slightly curved, lying parallel to the upper margin of hinge plate, C3 hooked, with posterior end swollen. Lateral teeth short, moderately swollen, inner and outer laterals of right valve approximately same size.

Anatomy. One siphon. Inhalant mantle opening merged with pedal slit, but retractors well developed (Fig. 29E). Mantle edge rather narrow. Inner radial mantle muscles weak, forming five well-distinguished bundles. Outer demibranch absent. Brood pouch placed dorsally, formed

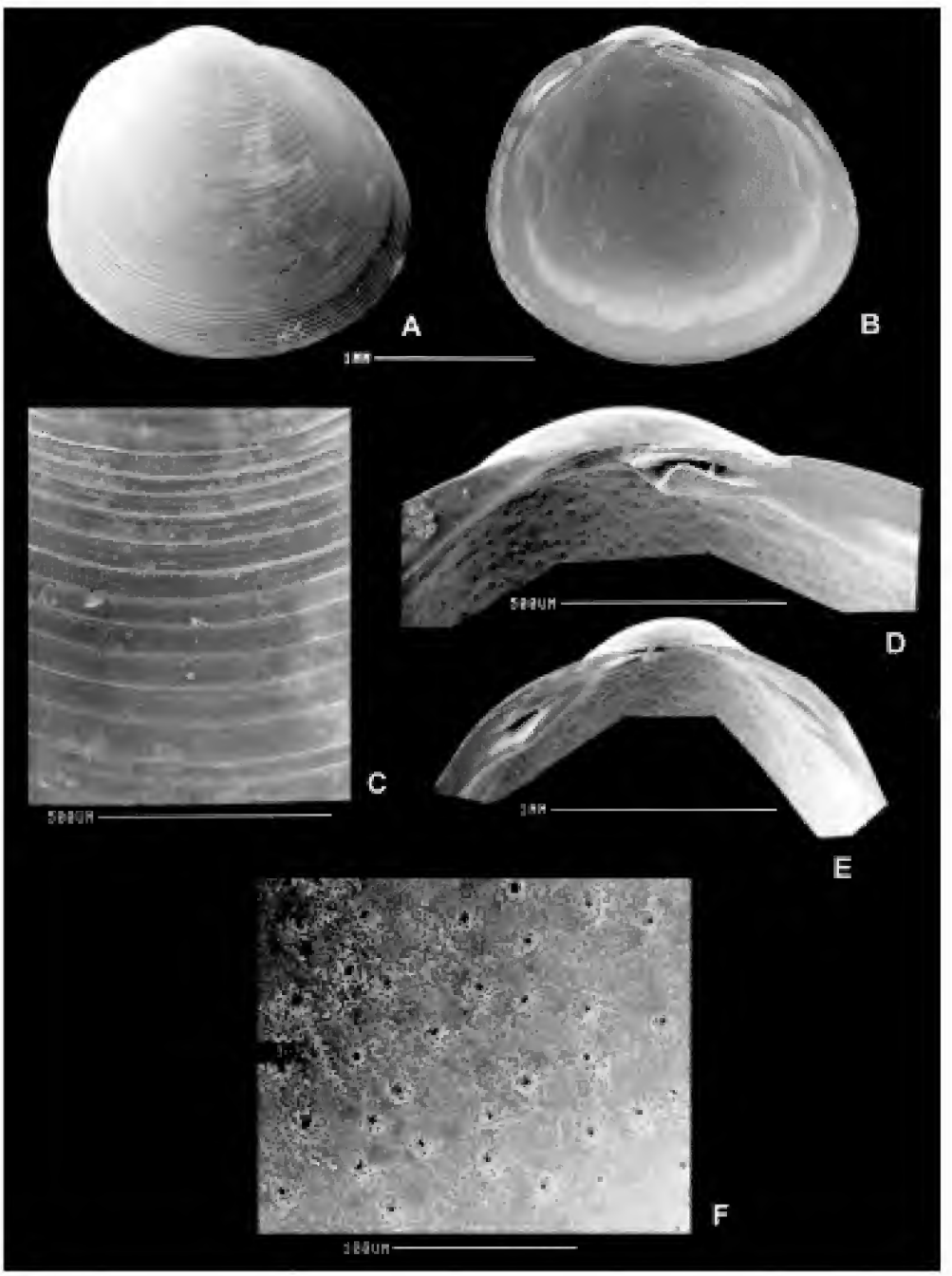


Figure 28. *Pisidium australiense* n.sp., type specimens, shell: A—right (from outside) and B—left (from inside) valves of the holotype (AM C350022); C—sculpture of the holotype, D—hinge (left valve of the holotype, right valve of the paratype); E—internal pores of the paratype (AM C350023).

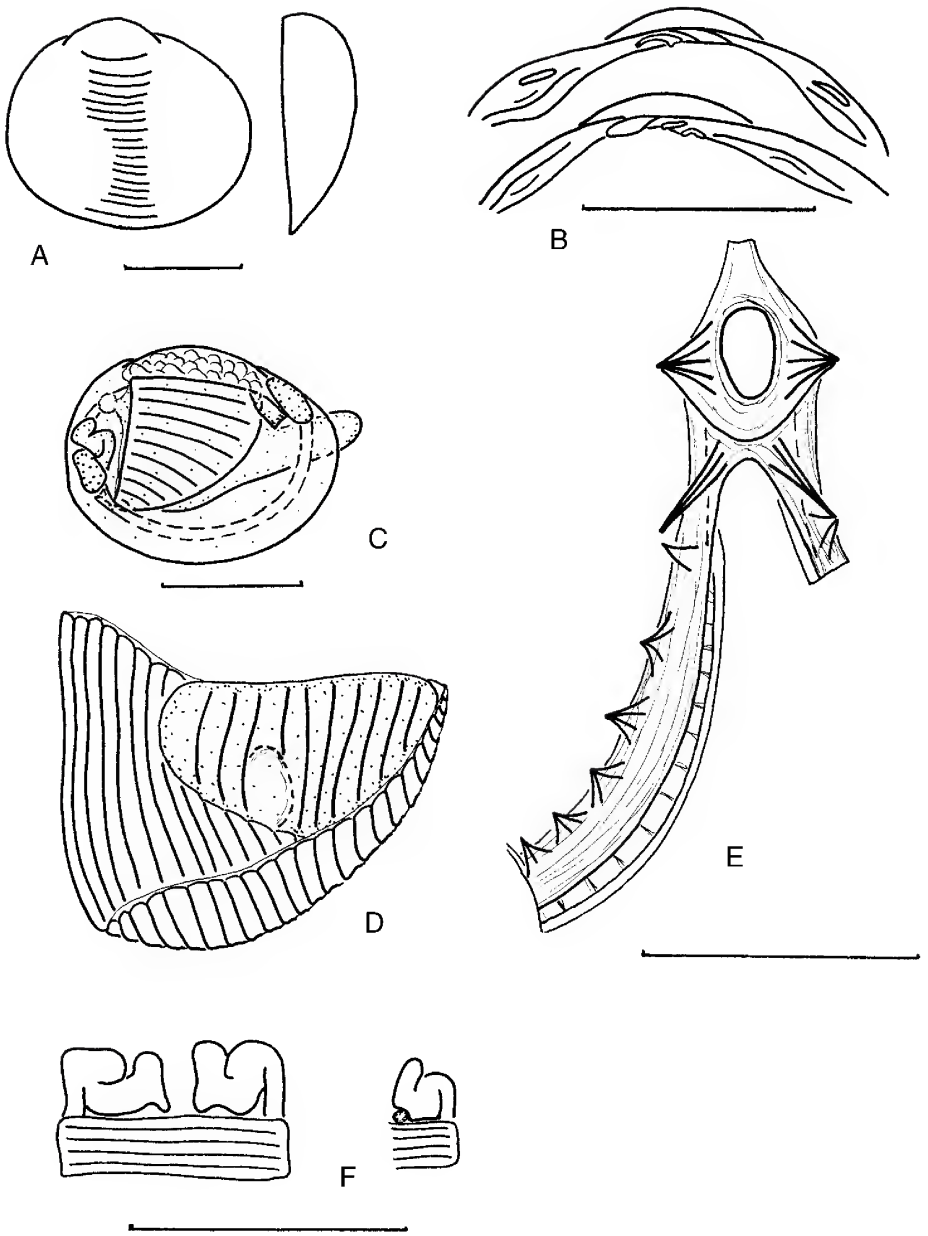


Figure 29. *Pisidium australiense*, paratypes (AM C350023), shell and anatomy: A—right valve, B—hinge, C—gross anatomy, D—ctenidium, E—mantle muscles, F—nephridia dorsally. Scale bars = 1 mm.

by seven to twelve filaments and containing two to six embryos. Nephridia of closed type, with clearly visible lateral loop (Fig. 29F).

Distribution. Known from several localities in northern Queensland, near Cairns (Fig. 57A).

Ecology. Inhabits springs and small creeks that are well shaded by trees with the bottom covered by leaves and vegetation.

Etymology. This species name is based on the country locality.

Taxonomic remarks. The presence of *Odhneripisidium* in Australia was suspected by Kuiper (1983), but this is the first species of the group to be described from the continent. A species of *Odhneripisidium* from New Guinea is mentioned, but not described, by him (Kuiper, 1983). Geographically nearby species inhabit the Sunda Archipelago (Indonesia) and New Britain (Kuiper, 1965, 1967). The new species is similar in shape to *P. dammermani* Odhner, 1940 from Sumba but differs in its regular concentric sculpture. *Pisidium sundanum* Rensch, 1934 from Java also has coarse sculpture, but is larger. The new species differs from *P. novobritanniae* Kuiper, 1967 (from New Britain), by having a rounded shell and more pronounced sculpture.

Subgenus *Euglesa* Leach in Jenyns, 1832

Type species. *Euglesa henslowiana* Leach in Jenyns, 1832 (= *Pisidium personatum* Malm, 1855), by monotypy.

Distribution. Cosmopolitan.

Diagnosis. Ligament enclosed, but not introverted. Inhalant opening of mantle and outer demibranch present. Brood pouch in low position (near upper edge of ascending lamella) and formed usually by four to five filaments, in largest specimens by six to seven filaments.

Remarks. While species of this group are distinguished from *Pisidium* s.str. (*P. amnicum* group) by the size and position of their brood pouch (Meier-Brook, 1970), many reviewers (e.g., Zeissler, 1971; Burch, 1975) consider it subgeneric. There has also been discussion concerning the name for this group. While the oldest name in consideration is *Euglesa* Leach, first published in synonymy by Jenyns (1832) and validated by publishing Leach's original manuscript (Leach, 1852). Despite the quite obscure diagnosis, there are no formal objections to this name, and it is widely used in Russian literature since Pirogov & Starobogatov (1974). The other names in use are *Cymatocyclas* Dall, 1903 (Zeissler, 1971), *Cyclocalyx* Dall, 1903 (Burch, 1975) and *Casertiana* Fagot, 1892 (Adler, 1994).

Pisidium (Euglesa) etheridgei E.A. Smith, 1883

Figs. 30–33

Pisidium etheridgei E.A. Smith, 1883: 306, pl. 7, fig. 35.
Australpera mena Iredale, 1943b: 95, fig. 3.
Pisidium casertanum.–Kuiper, 1983 (full Australian synonymy).
Pisidium carum.–Kuiper, 1983: fig. 54.

Type material. LECTOTYPE BMNH 1878.2.15.5 (Kuiper, 1983: 31), Yan-Yean Reservoir, Plenty District, Vic. PARALECTOTYPES BMNH, the same number and data as holotype, 4 specimens.

Australpera mena, lectotype (Kuiper, 1983: 32) AM C63905 and 4 paralectotypes AM C151006, Armidale, NSW.

Other material examined. QUEENSLAND: 1.5 km section of Gap Ck, off Glengallan Ck, Cunninghams Gap, Cunningham Hwy., 33 km E of New England Hwy, Qld, 28°03'S 152°23'E, alt. 720–680 m, on leaves in pools, coll. WFP, J. Stanisic & OG, 16 March 1981 (AM C313608d). NEW SOUTH WALES: Scrub Yard Ck NW of Little Mt Spirabo, 29°19'S 152°07'E, alt. 1045 m, coll. WFP, 1981 (AM 128706d); Unumgar State Forest, 28°25'S 152°41'E, coll. WFP, 1981 (AM C128678d); Dawsons Spring, Mt Kaputar, 30°17'S 150°09'E, alt. 1343 m, in sedges from spring source, coll. P. Colman, 8 November 1983 (AM C140422d); Solomons Ck, Erlen Bog State Forest, Glen Allen, 36°44'S 149°30'E, coll. WFP & JH, 14 February 1983 (AMw); 1/2 km north of Alpine Ck on Snowy Mountains Hwy, Mt Kosciusko NP, small swampy creek, coll. WFP & JH, 1 November 1980 (AM C126962d); Bobundara Ck at road crossing, 29 km south of Cooma on Myalla Rd, 36°30'S 149°07'E, alt. 900 m, coll. GC, 4 November 1990, with *Pisidium ponderi* n.sp. (AM C315743w). VICTORIA: Chinamans Ck, Wilsons Promontory NP, 38°55'S 146°24'E, alt. 80 m, in leaves, coll. WFP, A. de Keyzer & GC, 14 February 1990 (AM 315741w); tributary of Kinchington Ck near Bruarong, 36°25'S 146°50'E, alt. 540 m, coll. JW & GC, 6 December 1988 (AMw); tributary of Morwell River, 38°11'S 146°20'E, coll. WFP & GC, 20 February 1987 (AMw). SOUTH AUSTRALIA: Larrakin Lagoon, Kangaroo Island, Cotton coln. (SAM D3587d); Evens Ponds, near Mt Gambier, sediment near outflow (AMw); Portland-Nelson Rd, 38°11'S 141°19'E, coll. WFP, 15 May 1984 (AMw). TASMANIA: Launceston (AM C109827), identified by Kuiper as *P. carum*; Thirteen Mile Ck, tributary of Hazelwood River at Mt Cleveland-Corinna road junction, flowing large steam, coll. WFP, WP & JH, 24 January 1982 (AM C135175w), north of Ben Lomond Rd near Legges Tor Pond with small stream inflow, coll. WFP, WP & JH, 18 January 1982, (AM 135189w); tributary of East Gawler River, near Castra Rd, coll. 19 January 1982 by WFP & JH (AM C135196w); Lake Malbena, 41°57'S 146°16'E coll. JW, 3 February 1988, with *P. fultoni* (AMw); Lake Butters, 41°48'S 146°26'E, coll. JW, 5 February 1988, with *P. fultoni* (AMw); channel between Lake Sorell and Lake Crescent, 42°08'S 147°10'E, coll. S. Clark & A. Miller, 10 February 1995 (AMw); Urquart Ck, New River Lagoon, 43°30'S 146°34'E, coll. JW, 15 February 1988 (AMw).

Diagnosis. Shell short oval or quadrangular, moderately convex. Surface irregularly striated. Pores moderately dense. Hinge plate relatively narrow. Cardinal teeth arched or bent. Presiphonal mantle suture elongated. Inner radial mantle muscles form five to seven strong bundles. Outer demibranch small, strongly shifted posteriorly.

Shell rather small, but larger than in other species of *Pisidium* (sometimes more than 5 mm long), short-oval or quadrangular, moderately convex, usually of moderate thickness, but in some populations rather thin and fragile. Mean value of height index (H/L) for population not less than 0.81, typically 0.83–0.84 (Table 3). Margins rounded, sometimes with obtuse angles at extremities of upper margin. Most extended point of front margin approximately at level of horizontal median plane. Umbones broad, not protruding, considerably shifted posteriorly (placed at posterior 0.45 of shell length). Surface irregularly striated. Pores density variable between populations, usually not exceeding 450 per mm^2; mean value 254±107 (n = 20). Scars of most anterior muscle bundles always separated from mantle line, posterior scars sometimes merged with latter.

Hinge plate of moderate and even breadth. Ligament pit rather long and narrow. Cardinal teeth: c2 arched or bent in middle point, c4 straight or slightly arched, obliquely placed behind c2, c3 also bent or arched, thickened and cleft on posterior end with two parts adjoining each other. Lateral teeth narrow, not swollen, outer lateral teeth in right valve almost of same length as inner ones.

Anatomy. Mantle edge thick and broad. Presiphonal suture apparently elongate, 1/5 to 1/4 length of pedal slit (Figs. 33H–M, 34A). Mantle musculature well developed. Inner radial mantle muscles long (longer than outer radial ones), strong, number of bundles variable (five to seven) due to their merging or splitting.

Outer demibranch small (Figs. 33B–F, 34B), anterior edge placed at 11th to 14th filament of inner demibranch in most populations except several where outer demibranch greatly reduced; mean value for pooled data 12.8±0.38 (n

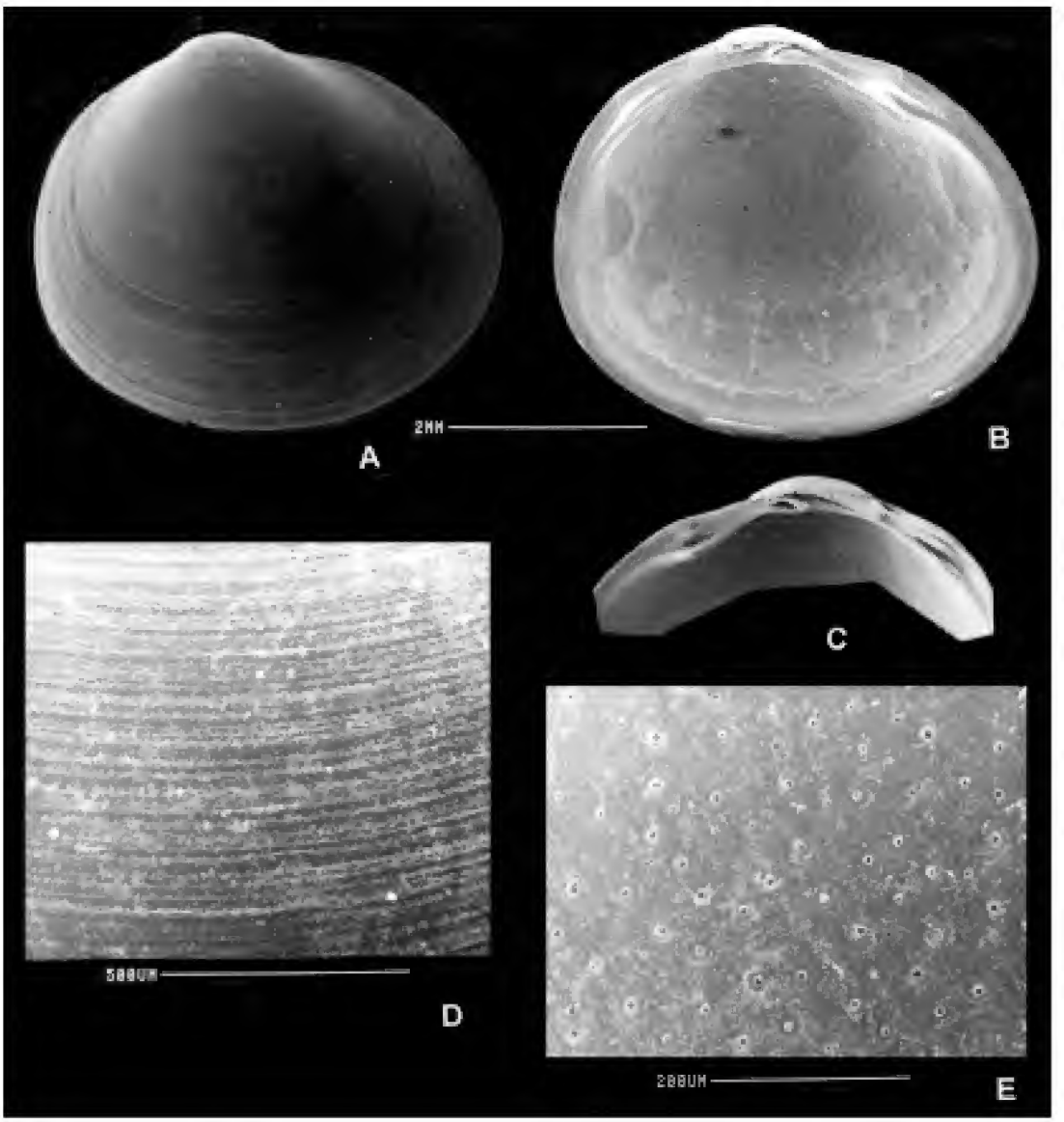


Figure 30. *Pisidium etheridgei* (E.A. Smith), Chinamans Ck, Wilsons Promontory, Vic. (AM C315741), shell: A—right valve from outside, B—left valve from inside, C—hinge of the right valve, D—sculpture, E—internal pores.

= 41). The brood pouch formed by four to seven filaments, five-filament pouches found most often. Number of offspring extremely variable: from one to ten in each demibranch, usual number four to eight.

Nephridium of closed type; dorsal lobe rectangular (Fig. 33G).

Distribution (Fig. 57B). The most southern part of Queensland, eastern NSW and Victoria along the Great Dividing Range, southeastern South Australia (including Kangaroo Island) and Tasmania. It is recorded for the Murray system by Gabriel (1939), but no material from that area has been seen and therefore these records need checking. A wider distribution in Queensland seems probable given the paucity of collections from that state.

Variability. This is one of the most variable species of *Pisidium*. Variability of shell characters have a geographic pattern, but differences between local forms are not as clear as in *Musculium tasmanicum*. The form typified by the type of *Australpera mena* Iredale, occurring in southern Queensland and northern NSW, is characterised by a rounded or oval shell with a rather high hinge plate and coarser sculpture (Fig. 32A–D). Specimens from Mt Kaputar (Fig. 32E,F) share these characters but are distinguished by their larger size (the largest specimen: L 5.7, H 4.6, W/2 1.6 mm) and numerous embryos per pouch (up to 10).

In many specimens from southern New South Wales (Snowy Mountains) and mountains of Victoria sculpture is weak, umbones are strongly shifted posteriorly, and hinge

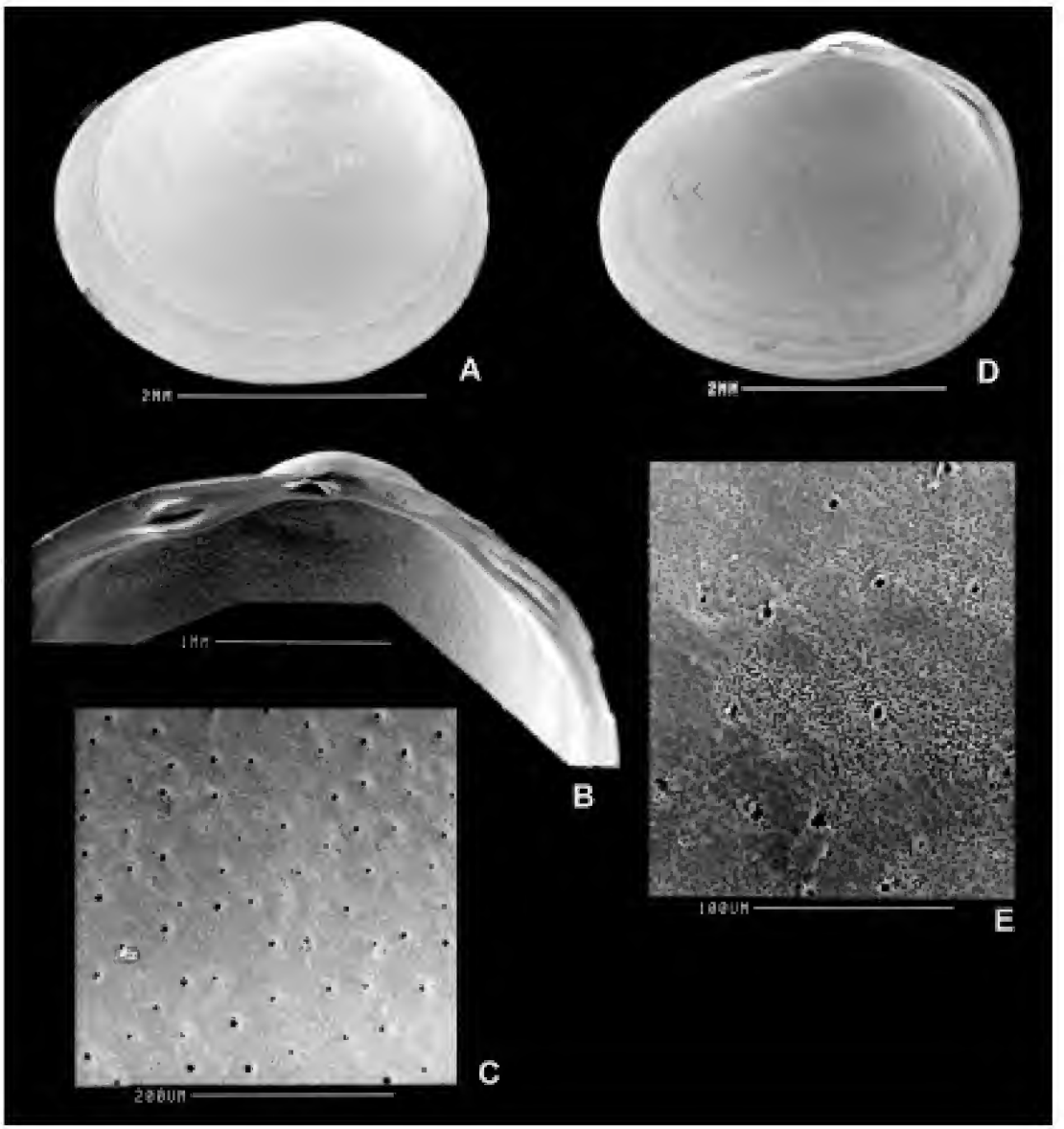


Figure 31. *Pisidium etheridgei*, shells: A–C—Bobundara Ck, NSW (AM C315743): A—left valve from outside, B—hinge of the right valve, C—pores; D,E—Lake Malbena, Tas. (AM, no number), D—right valve from inside, E—internal pores.

plate is rather narrow. Specimens with extreme outer demibranch reduction (anterior edge at 18th to 20th inner demibranch filament) were found in Bobundara Ck near Cooma (Figs. 31A–C, 33C). Another interesting abnormality observed in this area was irregularity of filament growth causing fusion of the filaments in the anterior part of the gill.

In the coastal area of Victoria and southeastern South Australia, an angulate, compressed form (the nominate one) with a strong hinge is the most common. Specimens characterised by circular and rather convex shells with a narrower hinge plate as well as by the concentration of the muscle bundles were also found here (Figs. 32G,H, 33K). In these characters, they are similar to *P. tasmanicum*, though differing in their larger size; their taxonomic placement is therefore disputable.

Tasmanian populations differ from those from the mainland in having more convex shells with broad, protruding umbones (Fig. 32I,J), some populations have large specimens (about 5.5 mm long). The characters of this form are the most pronounced in samples from southeastern Tasmania, where *P. etheridgei* looks like large *P. tasmanicum* (Fig. 32K). A peculiar form inhabits the lakes of central Tasmania, together with *P. fultoni*. This form is elongate, with a thin and fragile shell, narrow hinge plate (Fig. 31D,E) and incubates only a few embryos (one or two per pouch). The latter peculiarity is shared by *P. fultoni* associated with *P. etheridgei* in many Tasmanian lakes.

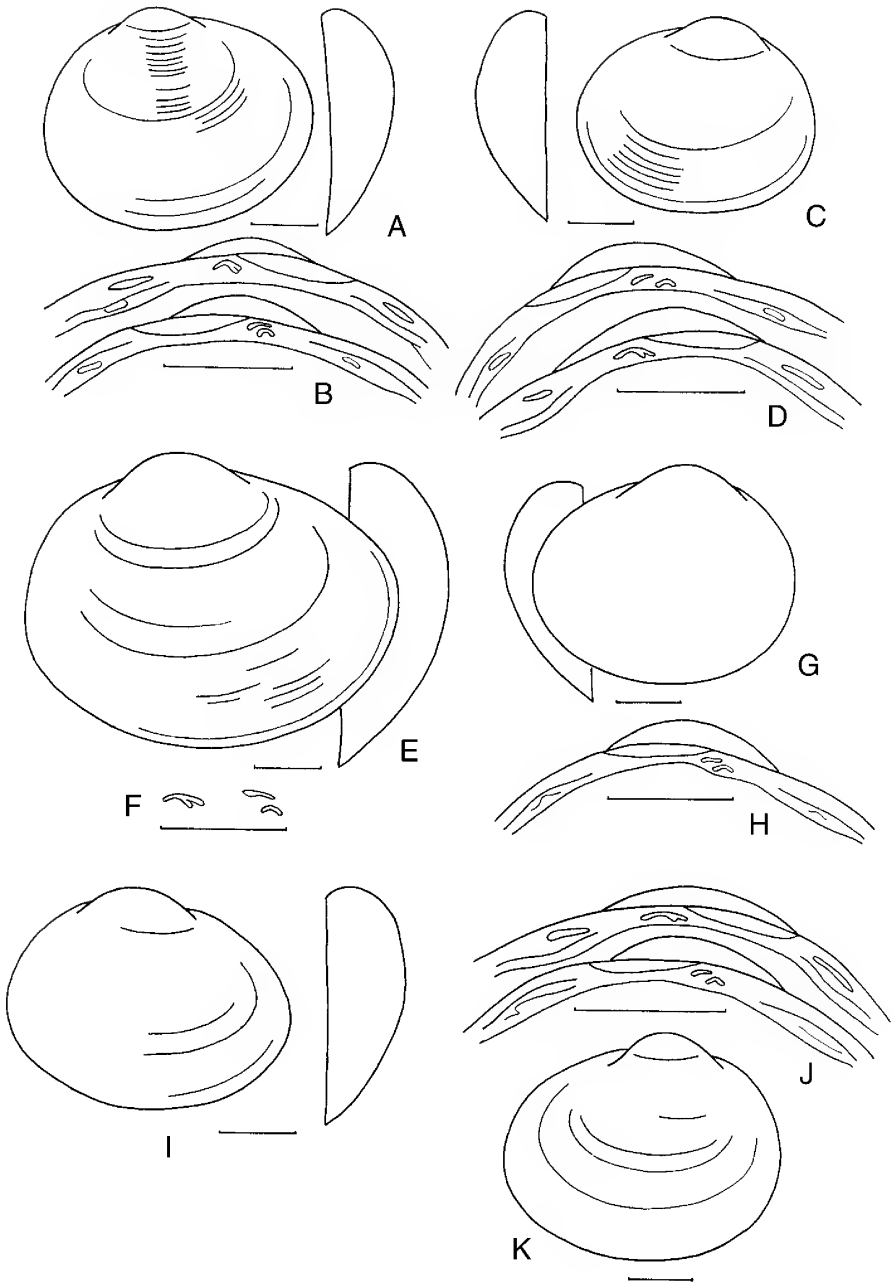


Figure 32. *Pisidium etheridgei*, variation of shell form: A,B—Gap Ck, southern Qld (AM C313608), right valve and hinge; C,D—Mt. Spirabo, NSW (AM C128706), left valve and hinge; E,F—Mt. Kaputar, NSW (AM C135175), E—right valve, F—cardinal teeth; G,H—tributary of Morwell River, Vic. (AM, no number), left valve and hinge of the left valve; I,J—Thirteen Mile Ck, Tas. (AM C135175), right valve and hinge; K—Urquart Ck, Tas. (AM, no number), left valve. Scale bars = 1 mm.

Ecology. Most frequent in creeks and small rivers. In South Australia and Tasmania it also inhabits lakes and lagoons.

Remarks. The affinity of *P. etheridgei* to the Eurasian *Pisidium casertanum* Poli, 1791 is controversial: some authors since E.A. Smith (1886) considered the Australian species distinct (Iredale, 1943a,b; Boettger, 1961), but Kuiper (1983) synonymises it with *P. casertanum*. These two species are certainly difficult to distinguish using shell characters. However, the shell of *P. casertanum* is usually triangular or subtriangular (the most extended point of the front margin is below the horizontal median plane), while in *P. etheridgei* the shell is oval or tetragonal. The umbones of the latter species are on average more central, placed perpendicular to the long axis of the shell. Because of the placement of the

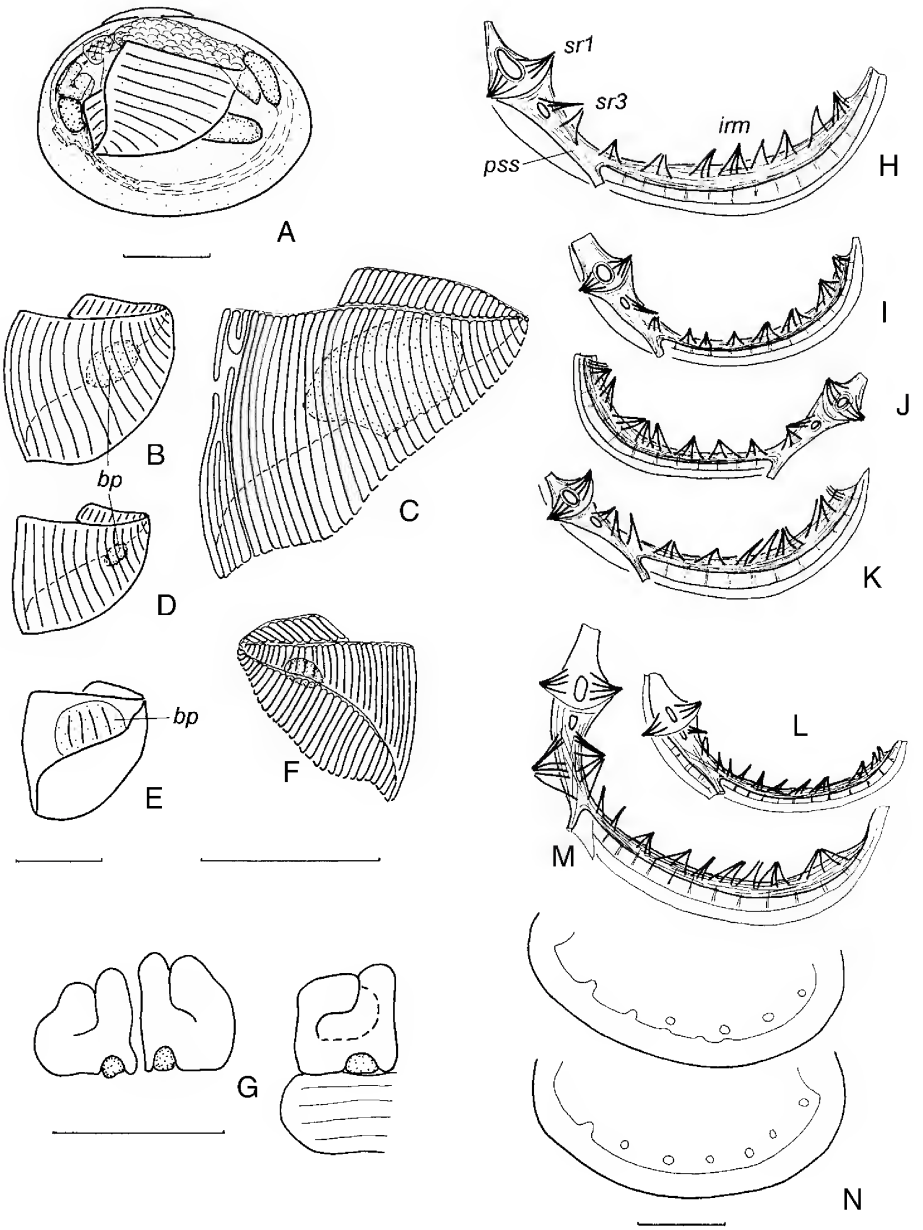


Figure 33. *Pisidium etheridgei*, anatomy: A—gross anatomy, Thirteen Mile Ck, Tas. (AM C135175); B–F—gills, B—Mt Kaputar, NSW (AM C135175), C—Bobundara Ck, NSW (AM C315743), specimen with abnormalities in filament growth, D—Chinamans Ck, Wilsons Promontory, Vic. (AM C315741), E–F—Thirteen Mile Ck, Tas. (AM C135175); G—nephridia dorsally, Thirteen Mile Ck, Tas.; H–M—musculature of the mantle edge, H—Mt Kaputar, NSW, I–J—Bobundara Ck, NSW, K—tributary of Morwell River, Vic.; L,M—Thirteen Mile Ck, Tas.; N—mantle muscle scars, Thirteen Mile Ck, Tas. Scale bars = 1 mm.

umbones and the similar form and position of the anterior and posterior lateral teeth, the shell of *P. etheridgei* is almost symmetrical, as mentioned by E.A. Smith (1883). In *P. casertanum*, the umbones are strongly shifted and bent towards the hind end of the shell, the posterior lateral teeth are shorter than the anterior ones and the shell is markedly asymmetrical. In addition, in *P. etheridgei* the ligament pit is long, the posterior lateral teeth are thin and lie parallel to each other and the margin of the hinge plate, the outer and inner laterals are almost equal in length, whereas in *P. casertanum*, the laterals tend to be swollen and lie obliquely, outer laterals are shorter than the inner ones and form an acute angle with them. On the average, *P. casertanum* is characterised by the rather high density of the internal shell pores (up to 1000 per mm^2) (Korniushin, 1996b), their been markedly lower in *P. etheridgei*. However, the best diagnostic character is the markedly elongate presiphonal suture in *P. etheridgei*.

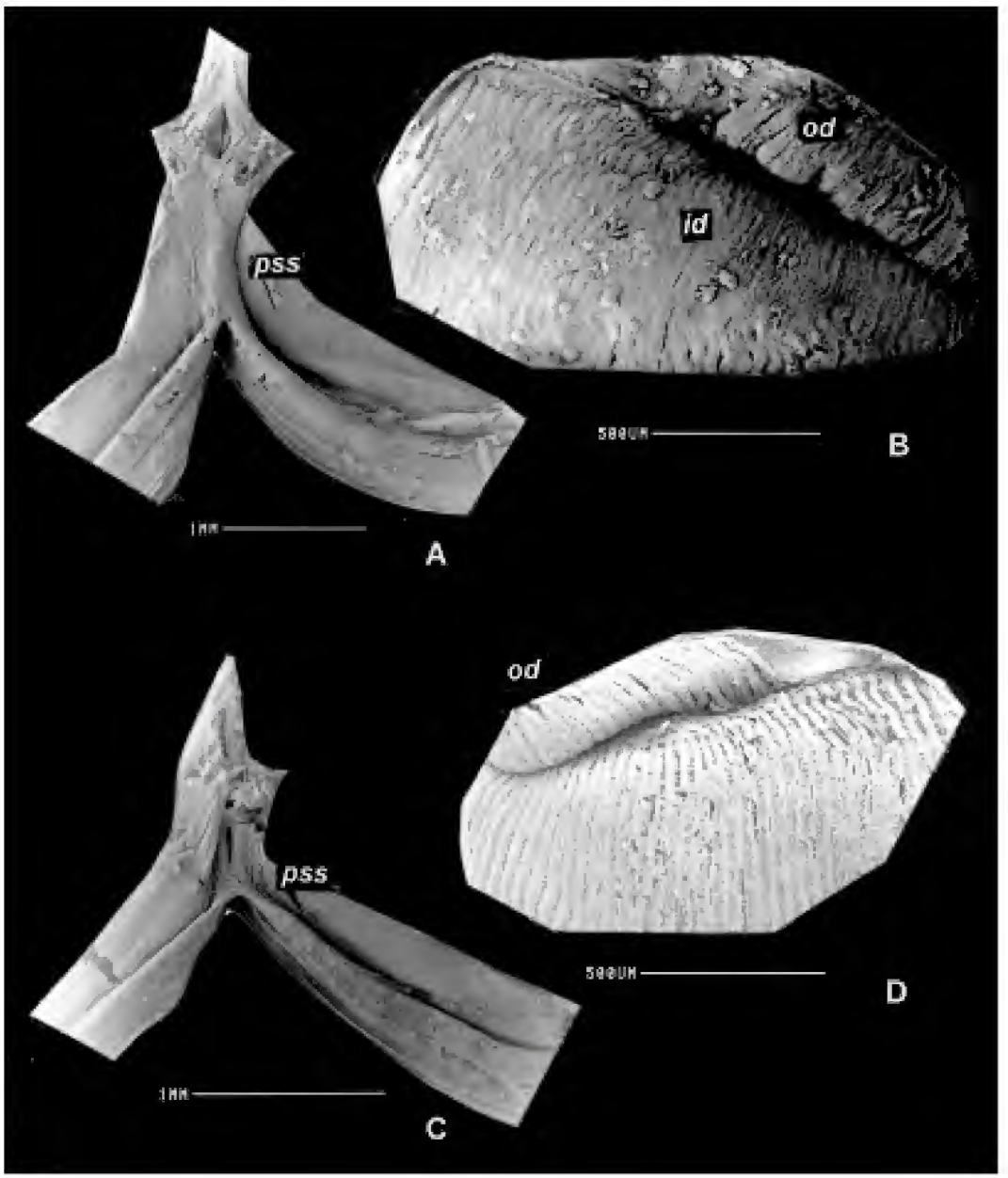


Figure 34. Soft body structures of some *Pisidium etheridgei* in comparison with *P. carum*: A—*Pisidium etheridgei* (E.A. Smith), Solomons Ck, NSW (AM, no number), part of the mantle edge; B—upper part of ctenidium from the same specimen; C,D—*P. carum*, Molong Ck, NSW (AM, no number), mantle edge and ctenidium.

Similar elongation of the presiphonal suture was observed in *Pisidium floresianum* Rensch, 1934 (Fig. 35) from the Flores Island and New Guinea. This species is also similar to *P. etheridgei* in its median position of the umbo and in the form of the hinge teeth. Another species similar to *P. casertanum* but with a more pronounced elongation of mantle suture, is known from the Amur River (East Russia) under the name *P. khurbaense* (Zatravkin, 1987) (Korniushin, 1996b).

Pisidium (Euglesa) hallae Kuiper, 1983

Figs. 36–38

Pisidium hallae Kuiper, 1983: 33, fig. 78–81.

Type material. HOLOTYPE AM C126964, Yarrangobilly River at Cave Rd, off Snowy Mountains Hwy, 35°23'S 148°30'E, NSW. PARATYPES AM C135457, 23 specimens examined by this study; other paratypes in BMNH (no number)*, SMF 192901*, ZMA K23050*, same data as holotype.

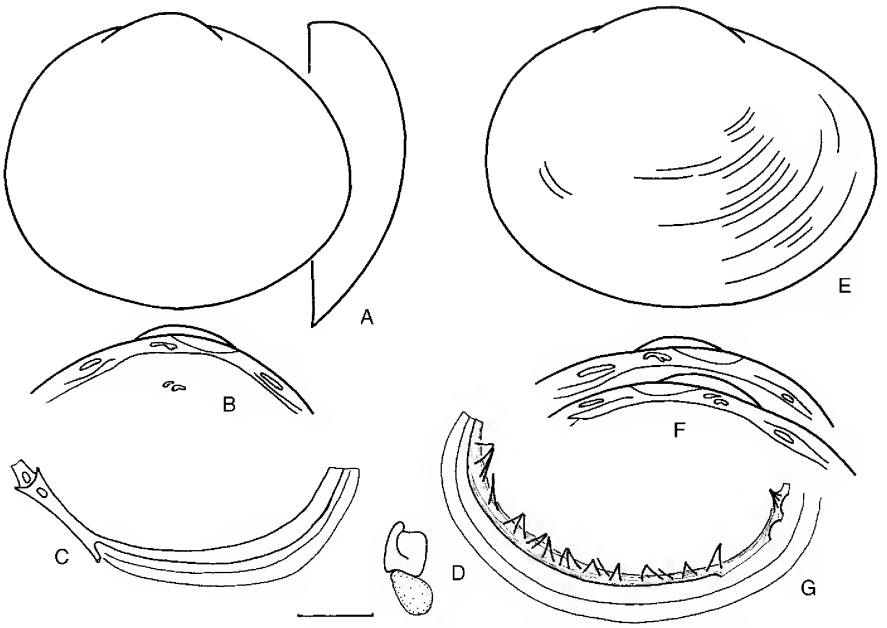


Figure 35. *Pisidium floresianum* Rensch, shell and anatomy: A,B—paratype, Flores Island (SMF), A—right valve, B—hinge of the right valve and cardinal teeth from the left one, C—mantle edge, D—nephridium (dorsally); E–G—Papua New Guinea (AM, no number), E—shell, F—hinge, G—dried mantle edge. Scale bar = 1 mm.

Other material examined. NEW SOUTH WALES: Four Mile Ck tributary, Ponderosa Forest Park, Nundle State Forest, 31°28'S 151°15'E, coll. WFP, 23 February 1988 (AM C315744w); swamp on Boggy Swamp Ck tributary, beside Pheasant Ck Rd, 2.5 km east of Thunderbolts Trail, Barrington Tops, 31°53'S 151°32'E, coll. WFP, 28 March 1985 (AM C314821w); Burraga Swamp, Barrington Tops NP, coll. WFP, 11 January 1982 (AM C135201w); Warranwang, west of Lithgow, Blue Mountains, 33°28'S 149°59'E, on grass, moss, etc., coll. WFP & AK, 18 August 1996 (AMw); the area of Kanangra-Boyd NP, coll. 1992 (AM C307115, AM C307128, AM C307130, AM C307133); Jinny Brothers Ck, 25 km south of Cooma, 36°27'S 149°07'E, coll. 4 November 1990 (AMw). VICTORIA: Mt Donna Buang Rd, 1.4 km from Warburton, 37°44'S 145°42'E, coll. WFP, JW & GC, 21 January 1987 (AMw). TASMANIA: tributary of Brid River near Springfield, 41°13'S 147°29'E., coll. WFP & R. Kershaw, 16 March 1975 (AMw); Ben Lomond Rivulet, 41°55'S 147°29'E, alt. 180 m, coll. WFP, JW & GC, 2 February 1987 (AMw); Franklin River, 42°31'S 145°45'E, coll. JW, 23 March 1988 (AMw).

Diagnosis. Shell elongate oval, moderately convex. Surface smooth. Pores rare. Hinge plate relatively narrow. Cardinal teeth arched or bent. Presiphonal mantle suture elongated. Inner radial mantle muscles form five to seven strong bundles. Outer demibranch small, strongly shifted posteriorly.

Shell. small (largest specimen: L 4.5, H 3.5, W/2 1.2 mm), oval, elongate, moderately convex, thin and fragile, subtransparent, periostracum usually of white or yellowish colour. Mean value of height index (H/L) for population not exceeding 0.78 (Table 3). All margins rounded, merging to each other without angles. The most extended point of front margin at level of horizontal median plane. Umbones broad, not protruding, considerably shifted posteriorly. Sculpture formed only by irregular growth lines. Pores relatively rare: mean density 239±43 per mm^2 (n = 5). Scars of muscle bundles separated from mantle line.

Hinge plate of younger specimens relatively narrow, in large shells somewhat broadened in area of ligament. Ligament pit long and narrow. C2 bent at middle point, in large specimens strongly curved (arched). C4 straight or slightly bent, placed obliquely behind c2. C3 strongly curved, thickened and cleft on posterior end with 2 branches adjoining each other. Lateral teeth rather short, parallel to margin of hinge plate; p2 terminating abruptly, with almost vertical hind edge, p1 and p3 narrow, almost of equal length.

Anatomy (Fig. 38). Mantle as in *P. etheridgei*. Presiphonal suture elongate, usually little more than 1/5 length of pedal slit. Pedal slit with six to seven long, strong muscle bundles; merging or splitting of latter also possible.

Outer demibranch strongly reduced and shifted posteriorly; usually beginning at 12th to 15th filament of inner demibranch (mean value for pooled data 13.3±2.3, n = 45).

Brood pouch formed by four to seven filaments, with four to seven embryos inside.

Nephridia of same shape as in *P. etheridgei*.

Variability. The species is less variable than *P. etheridgei*. Specimens from Tasmania have more protruded umbones then those from the mainland and are similar in this character to *P. tasmanicum* (see Figs. 75 and 85). The pattern of variability in the mantle muscle arrangement is not clear: most of the Tasmanian specimens are distinguished by the strong concentration of mantle muscles (five or six very

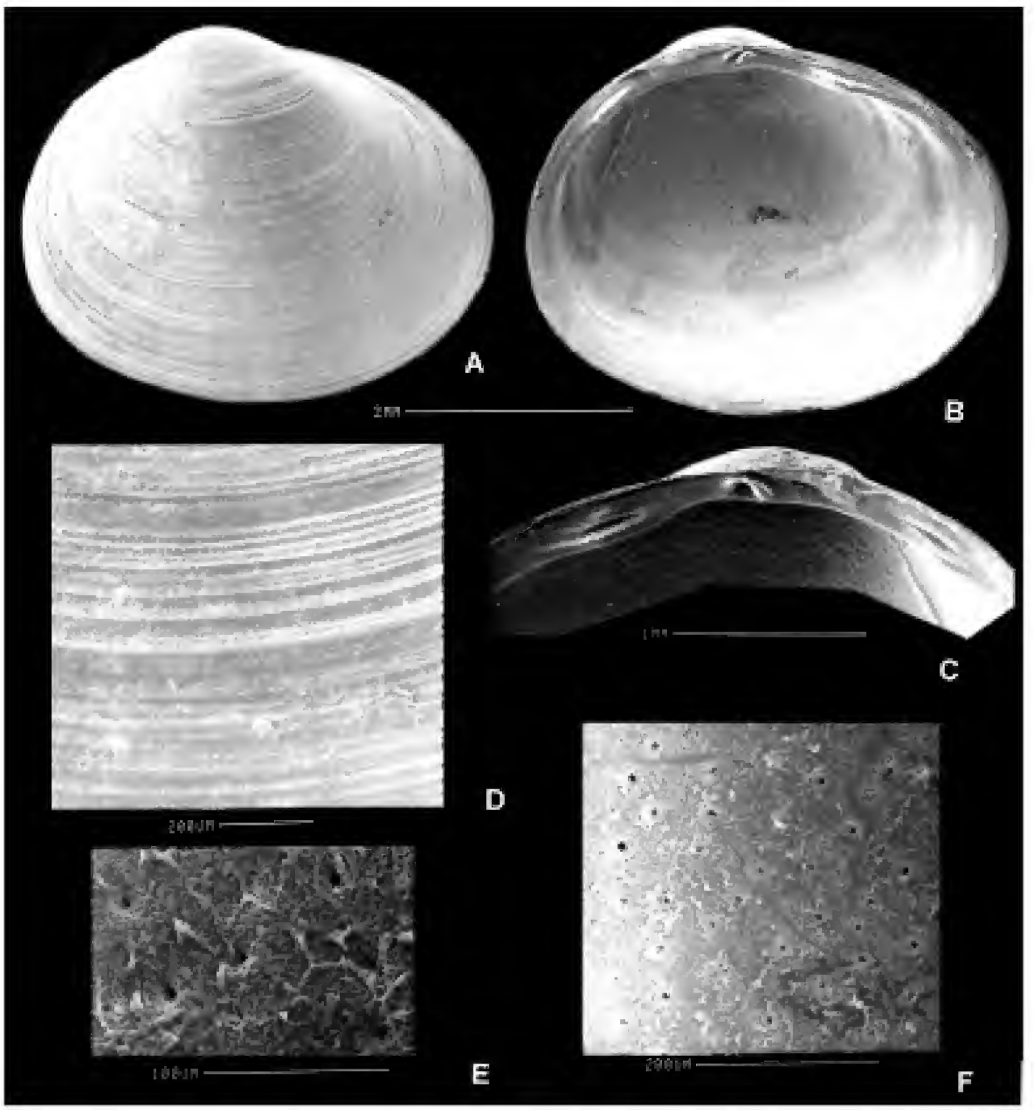


Figure 36. *Pisidium hallae* (Kuiper), Blue Mountains, NSW (AM, no number), shell: A—right valve from outside, B—left valve from inside, C—sculpture, D—hinge of the right valve, E,F—internal pores under different magnifications.

strong bundles), in New South Wales such specimens occur alongside those having many muscle bundles (up to ten) but are otherwise identical.

Generally, individual and interpopulational variability of the outer demibranch position is limited, but in some populations the outer demibranch is very strongly reduced, looking like a narrow stripe and beginning at 17th to 22nd filament of the inner demibranch. Specimens with the greatly reduced outer demibranch were found in the Snowy Mountains near the locality where a form of *P. etheridgei* with reduced outer demibranch was also found.

Distribution (Fig. 57B). This species is found along the Great Dividing Range in New South Wales and Victoria and in several localities in Tasmania.

Ecology. Swamps, springs and creeks.

Remarks. *Pisidium hallae* is most similar in shell and anatomical characters to *P. etheridgei*. It can be recognised mainly by its elongate shell (Kuiper, 1983). However, the height index (H/L) slightly overlaps *P. etheridgei*, and only large series can be identified reliably. The two species are well separated geographically, but contact zones in northern NSW, Snowy Mountains, Victoria and Tasmania are apparent. However, the two species were found together only in one locality (Alpine Ck). *Pisidium etheridgei* and *P. hallae* are clearly closely related species and a further investigation is needed to confirm reproductive isolation between them and explain the mechanism of this isolation.

Presence of *P. hallae* in Franklin River needs to be confirmed (available specimens are similar to *P. tasmanicum* and may represent a peculiar form of the latter species).

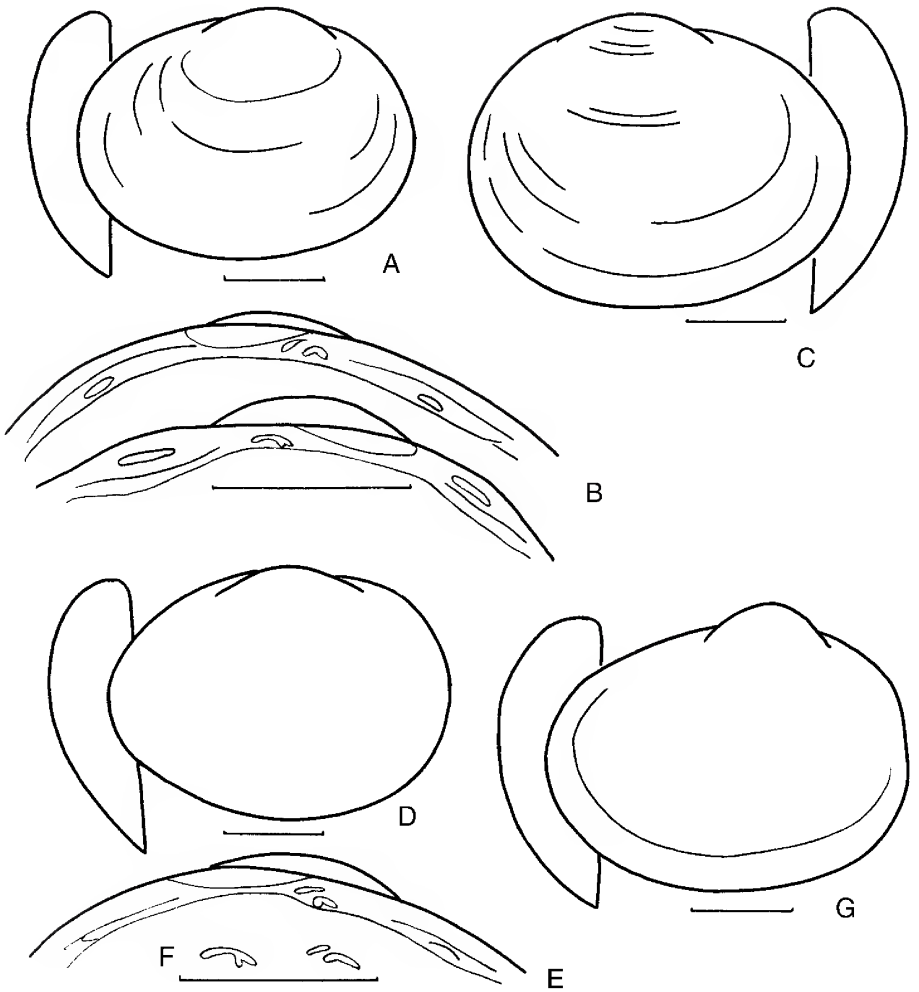


Figure 37. *Pisidium hallae*, shells: A,B—Nundle State Forest, NSW (AM C315744), left valve and hinge; C—Barrington Tops, NSW (AM C314821), right valve; D,F—Warburton, Vic. (AM, no number), left valve and hinge of the left valve, cardinal teeth of right and left valves; G—Ben Lomond Rivulet, Tas. (AM, no number), left valve. Scale bars = 1 mm.

Pisidium (Euglesa) kosciusko (Iredale, 1943a)

Figs. 39, 40

Glacipisum kosciusko Iredale, 1943a: 197.
Pisidium kosciusko.–Kuiper, 1983 (full synonymy).

Type material: HOLOTYPE AM C100523d, Blue Lake, Mt Kosciusko, NSW. PARATYPES AM C20790, AM C21790, about 40 specimens, same data as holotype.

Other material examined: NEW SOUTH WALES: Lake Albina at south end, depth 2 m, Mt Kosciusko NP, coll. B.V. Timms, 8 February 1977 (AM C315739w).

Diagnosis. Shell circular or short oval, moderately convex. Surface irregularly striated. Pores rare. Hinge plate very narrow. Cardinal teeth straight or slightly bent. Presiphonal mantle suture slightly elongated. Inner radial mantle muscles form five to seven strong bundles. Outer demibranch small, strongly shifted posteriorly.

Shell: Small (largest specimen 4.3 mm long), circular or short oval, flat or moderately convex, thin, subtransparent. Upper margin arched, angles at its extremities not clear, other margins evenly curved. Umbones low and broad, not protruding. Sculpture faint, represented by irregular striae; larger specimens with pronounced lines of growth breaks. Internal pores relatively rare, mean density 258±114 per mm^2 (n = 6).

Hinge plate narrow. Ligament pit elongate. C2 and c4 almost straight, parallel to each other; c2 shorter than c4; c3 slightly bent at middle point, cleft on posterior end. Lateral teeth narrow, outer laterals in right valve somewhat shorter than inner.

Anatomy. Mantle edge moderately broad. Presiphonal suture slightly elongate (about 1/5 length of pedal slit). Inner

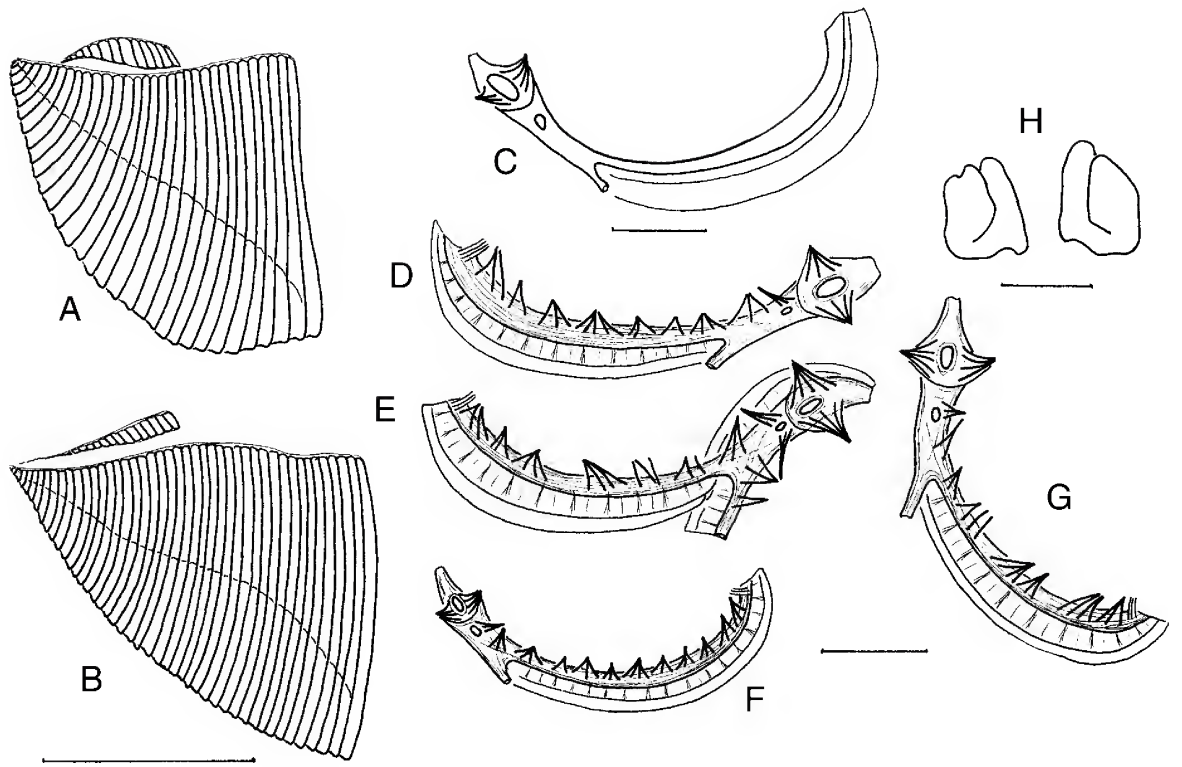


Figure 38. *Pisidium hallae*, anatomy: A,B—gills, A—Warburton, Vic. (AM, no number), B—Jinny Brothers Ck, NSW (AM, no number), a specimen with strongly reduced outer demibranch; C–G—mantle edge, C,D—Barrington Tops, NSW (AM C314821), E—Blue Mountains, NSW (AM, no number), F—Jinny Brothers Ck, NSW, G—Ben Lomond Rivulet, Tas. (AM, no number); H—nephridia dorsally, Barrington Tops, NSW. Scale bars = 1 mm.

radial mantle muscles weaker than in *P. etheridgei*, forming seven bundles along pedal slit.

Outer demibranch strongly reduced and placed against 12th or 13th filament of inner demibranch (mean value 12.8±0.5, n = 4). Brood pouches not found.

Nephridium of closed type, with rectangular dorsal lobe.

Distribution. Known from the area of Mt Kosciusko, Snowy Mountains, New South Wales.

Ecology. Abundant in two alpine lakes; Kuiper (1983) mentioned also several lots from creeks and pools.

Remarks. This species is the most similar to *P. etheridgei*. It differs from the latter having a very thin hinge plate, parallel cardinal teeth and the outer lateral teeth being shorter than the inner ones.

However, the mentioned characters considerably vary within the studied populations. This species occupies a very specialised habitat, where it replaces *P. etheridgei*. The probability of speciation in these small alpine lakes is rather low, while no other endemic species of molluscs are known from them. Therefore *P. kosciusko* may prove to be only a peculiar form of *P. etheridgei*.

Pisidium (Euglesa) tasmanicum Tenison Woods, 1876

Figs. 41–44

Pisidium tasmanicum Tenison Woods, 1876: 82; Kuiper, 1983: 26 (part: full synonymy, only Tasmanian localities).

Type material: POSSIBLE SYNTYPES TMH E112 (Kuiper, 1983), 43 valves, ?Browns River, Tas.

Other material examined: VICTORIA: east branch of Barwon River, on Seven Bridges Rd, 38°29'S 143°44'E, alt. 140 m, coll. FWA, 16 April 1988 (AM C317041w); Deep Ck east of Foster, South Gippsland, coll. GC, 11 January 1992 (AMw); Frasers Ck, Wilsons Promontory, 39°04'S 146°20'E, coll. JW & GC, 11 December 1988 (AMw); tributary of Morwell River, 38°31'S 146°20'E, coll. WFP & GC, 10 February 1987 (AMw). TASMANIA: North Esk River on Blessington Rd 1.2 km west of Musselboro Rd, east of Launceston, 41°30'S 147°25'E, alt. 315 m, coll. WFP, JH & WP, 18 January 1982 (AM C135155w); Geales Ck on a side track off NW side of Bass Hwy, 40°53'S 145°02'E, coll. WFP, WP & JH, 22 January 1982 (AM C135169w); Wandle River at Murchison Hwy, rock and gravel substrate, coll. WFP, WP & JH, 23 January 1982 (AM 135192w); Ben Lomond Rivulet, 41°55'S 147°29'E, alt. 180 m, coll. WFP, JW & GC, 2 February 1987,

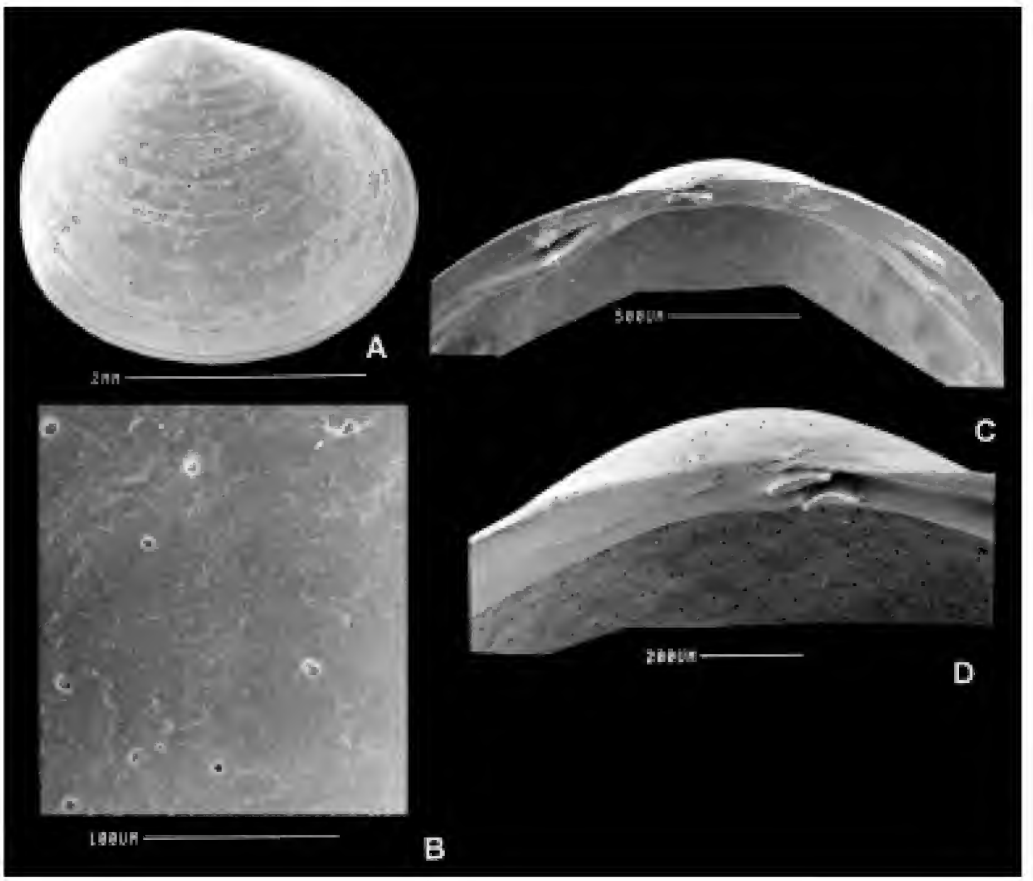


Figure 39. *Pisidium kosciusko* (Iredale), Lake Albino, Mt Kosciusko, NSW (AM C315739), shell: A—right valve from outside, B—pores, C—hinge of the right valve, D—cardinal teeth of the left valve.

with *P. hallae* (AMw); Nora River, tributary of Bird River, 25 km off Queenstown, 42°18'S 145°36'E, coll. S. Clark & A. Miller, 9 February 1995 (AMw); Lake Dulverton, R. Tate coln., undated, identified as *P. dulvertonensis* (SAM D19060d).

Diagnosis. Shell rounded or subtriangular, markedly convex. Surface irregularly striated. Pores of moderate density. Hinge plate narrow. Cardinal teeth slightly bent. Presiphonal mantle suture short or slightly elongated. Inner radial mantle muscles form four to six strong bundles. Outer demibranch small, strongly shifted posteriorly.

Shell: Small (largest specimen: L 3.6, H 3.1, W/2 1.2 mm), rounded or subtriangular, convex, thin and fragile, subtransparent, periostracum white, reddish or brownish. Upper margin short, usually marked by angles at its extremities. Hind margin obtuse, anterior one straight and oblique, with most extended point below horizontal median plane. Umbones moderately broad, protruding, definitely shifted backwards. Sculpture: clear, irregular striations and folds; coarser striae around umbones. In some populations sculpture reduced and shell almost smooth. Internal pores of moderate density: 310±84 per mm^2 (n = 8). Anterior muscle scars separated from mantle line.

Hinge plate short and narrow, arched. Ligament pit short. c2 slightly bent at middle point; c4 straight or slightly bent, almost parallel to margin of hinge plate; c3 thin, bent, cleft on its hind end. Lateral teeth short, outer ones in right valve shorter then inner.

Anatomy (Fig. 44). Mantle edge moderately broad. Presiphonal suture short or slightly elongate, 1/6 to 1/7 length of pedal slit, but in some specimens more elongate (1/5 length of the pedal slit). Mantle musculature strong, inner radial muscle bundles long but reduced in number. Four to six bundles visible at each side of pedal slit, strongest bundle second from anterior.

Anterior edge of outer demibranch placed at 10th to 16th, most frequently at 11th or 12th filament of inner demibranch. Mean value of this character 11.9±1.7 (n = 20). Brood pouch formed by four or five filaments. The number of larvae per pouch usually three to five, sometimes one or two.

Nephridia of same type, as in *P. casertanum* and *P. hallae*.

Variability. The lots from southern Victoria are distinguished by their small size (shell length not more than 3.2 mm), narrower umbones, thinner hinge plate, coarse striation (Fig. 41). Shells from northern Tasmania are also small, but with broader umbones and less pronounced sculpture (Fig. 42).

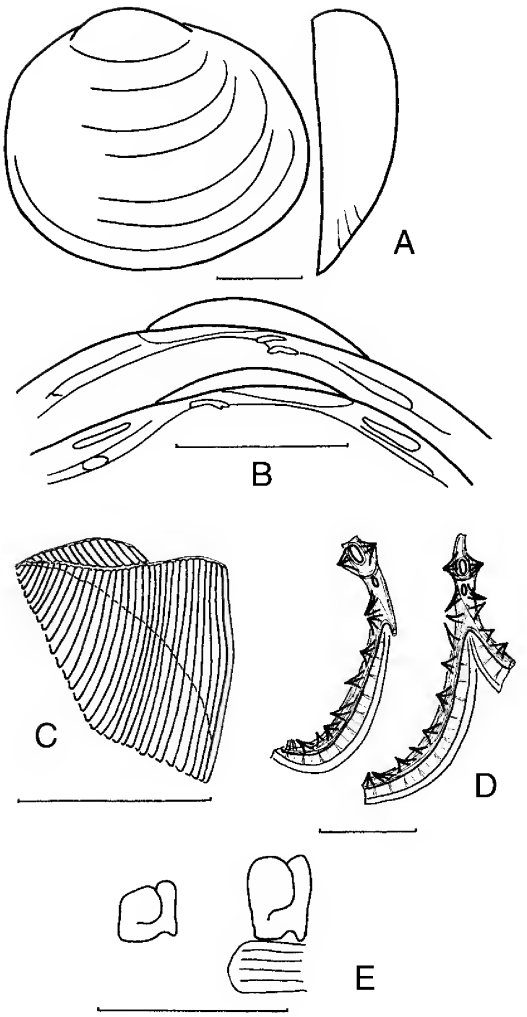


Figure 40. *Pisidium kosciusko*, shell and anatomy: A,B—holotype, Blue Lake, Mt Kosciusko, NSW (AM C100523), right valve and hinge; C–E—Lake Albino, Mt Kosciusko, NSW (AM C315739), C—gill, D—mantle edge, E—nephridia dorsally. Scale bars = 1 mm.

Southern Tasmanian lots (including the probable type lot) are relatively large (3.4–3.6 mm long), less convex, with broader umbones, more similar to *P. etheridgei* from this area (Fig. 43C,D,G). Some lots have intermediate characters (Fig. 43A,B,E,F).

Distribution. Southern Victoria and Tasmania (Fig. 57C).

Ecology. Creeks, occasionally in lakes (in Tasmania).

Remarks. The northern form of *P. tasmanicum* is readily distinguished from *P. etheridgei* by its smaller size, narrow and protruding umbones, narrow hinge plate, and cardinal teeth being thin and only weakly bent. However, some variation of all these characters takes place and reliable identification is only possible with a series of specimens. The situation in Tasmania, especially in its southern part, is more complicated. The local form of *P. tasmanicum* is larger and can be confused with *P. etheridgei* and *P. hallae*. In general, *P. tasmanicum* and *P. etheridgei* widely overlap in all shell indices and the differences in pooled data are not statistically significant. Anatomical distinction is also not reliable: concentrated mantle musculature, a characteristic feature of *P. tasmanicum*, does occur in *P. etheridgei*.

The differences between *P. tasmanicum* and *P. etheridgei* are much more pronounced when sympatric populations are compared. In all these cases it was possible to discriminate two species by shell size, convexity and length of the mantle suture. Unfortunately, there were insufficient specimens in the lots from sympatric populations for statistical treatment (usually only one species was abundant). When found together with *P. hallae, P. tasmanicum* can be distinguished by its circular, not elongate, shell (Figs. 37G, 43A,B). Thus, while consistently reliable characters separating *P. tasmanicum* and *P. etheridgei* are still lacking, in some sympatric localities the two species are readily separated. However, identification of some other local populations is rather difficult, and further investigation is required to resolve the relationships of these two taxa.

In the structure of the mantle musculature, *P. tasmanicum* is similar to the widely distributed Eurasian species *P. personatum* Malm, 1855 and *P. obtusale* (Lamarck, 1818). Some shell characters of these species are also similar (notably the rounded and swollen shell and thin hinge plate with straight cardinal teeth). However, the outer demibranch in *P. tasmanicum* is much more reduced than in *P. personatum* and *P. obtusale*.

Specimens from New South Wales identified by Kuiper (1983) as *P. tasmanicum* have another type of sculpture (regular ribs), which indicates their affinity to *P. carum*. These specimens are described below as the new species *Pisidium ponderi*.

Pisidium (Euglesa) fultoni Kuiper, 1983

Figs. 45, 46

Pisidium fultoni Kuiper, 1983: 34, fig. 74–77.

Type material: HOLOTYPE TMH E14436, East Lake (north), part of Arthurs Lake, Tas. PARATYPES TMH E14437*, AM C135460, NMV F31818*, BMNH*, SMF 192865, 20 specimens altogether, same data as holotype.

Other material examined: TASMANIA: Great Lake, Taffin coln., 2 June 1902, det. J. Kuiper as *S. lacusedes* (TMH E5194d); Lake Malbena, 41°57'S 146°16'E, coll. JW, 3 February 1988, with *P. etheridgei* (AMw); Lake Butters, 41°48'S 146°26'E, coll. JW, 5 February 1988, with *P. etheridgei* (AMw); Lake Olive, 41°56'S 146°20'E, coll. JW, 5 February 1988 (AMw); Lake Nugetena, near Lake Olive, 41°56'S 146°19'E, coll. JW, 2 February 1988 (AMw).

Diagnosis. Shell tetragonal or pentagonal, flat. Surface irregularly striated. Pores of moderate density. Hinge plate narrow. Cardinal teeth bent. Presiphonal mantle suture short or slightly elongated. Inner radial mantle muscles form five to six strong bundles. Outer demibranch small, strongly shifted posteriorly.

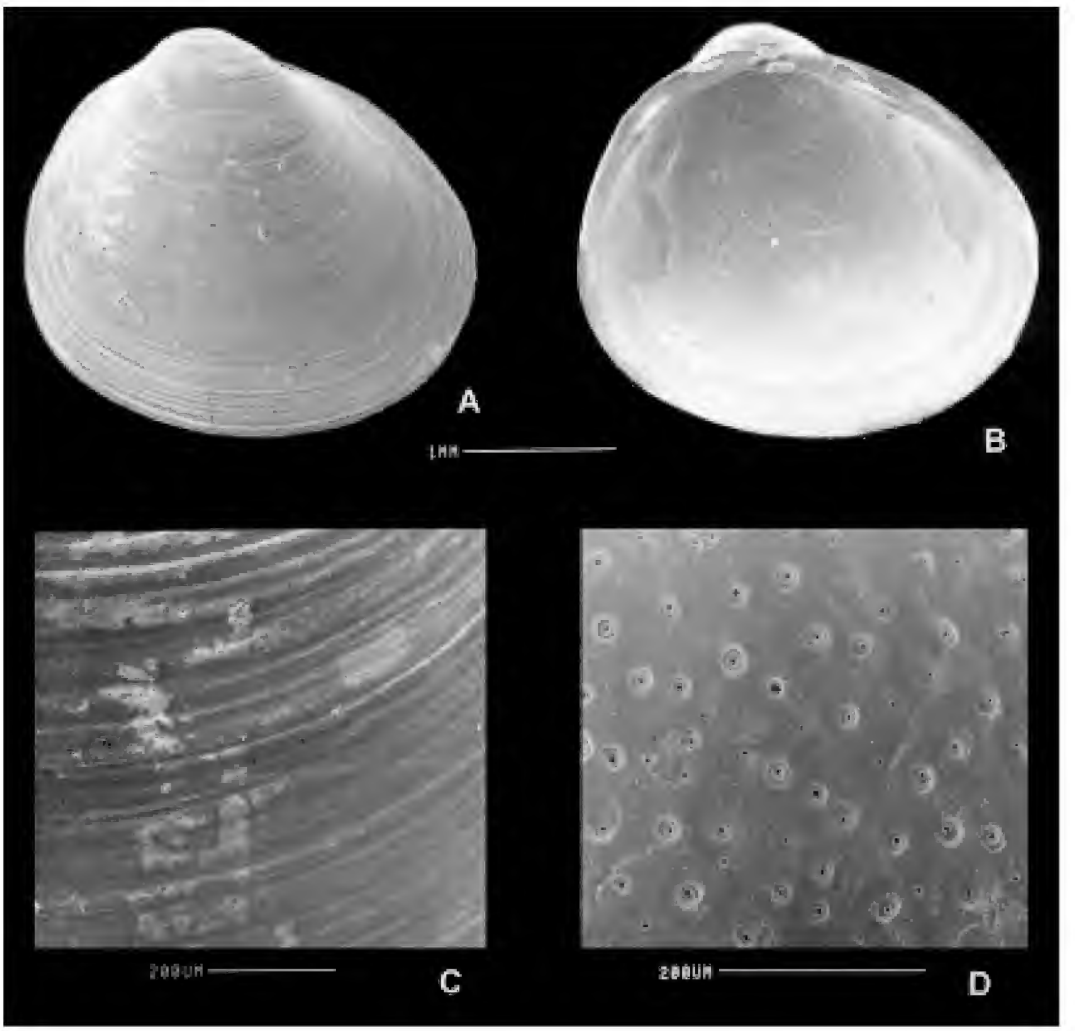


Figure 41. *Pisidium tasmanicum* (Tenison Woods), tributary of Morwell River, Vic. (AM, no number), shell: A—right valve from outside, B—left valve from inside, C—sculpture, D—internal pores.

Shell: rather small (largest specimen: L 4.6, H 4.0, W/2 1.2 mm), angulate (tetragonal or pentagonal), usually of somewhat irregular shape, thin, with characteristic yellow periostracum, flat. Upper edge straight, with clear angles at extremities, especially posteriorly. Hind edge straight, often oblique, sometimes with depressed outline. Front edge also straight, with most extending point below horizontal median plane. Hind edge often bent forward, almost parallel to front one. Umbones moderately shifted posteriorly, narrow in young specimens and relatively broad in large shells. Sculpture: weak irregular striations and growth lines. Internal pores rather numerous: mean density 457±210 per mm^2.

Hinge plate narrow. Cardinal teeth thin, c4 and c3 evidently bent, c3 cleft posteriorly. Lateral teeth thin, outer teeth in right valve shorter than inner, sometimes reduced.

Anatomy. Mantle edge broad. Presiphonal suture variable (from 1/7 to 1/4 length of pedal slit). Inner radial mantle muscles long and strong, more concentrated than in *P. etheridgei*, usually five to six bundles distinguishable.

Outer demibranch anterior edge placed at 10th to 13th filament of inner demibranch (mean value 10.8±1.0, n = 4). Gravid specimens with one or two free larvae in each demibranch, brood pouches not seen.

Nephridium of closed type, with rectangular dorsal lobe.

Variability. Variability of the shell outline in this species is remarkable, even amongst individuals inhabiting one lake. Quite often the shell outline is distorted, with angles or depressions, which may be caused by irregularities of growth or deformation (Fig. 46E,F). Variability in mantle and gill characters is also notable.

Distribution. Found only in central Tasmania (Fig. 57B).

Ecology. Found only in lakes, abundant in littoral samples, presence in deeper benthos not clear.

Remarks. As shown here, *P. fultoni* may have a much larger size than previously realised (Kuiper, 1983). The larger specimens are conspecific judging from young shells from

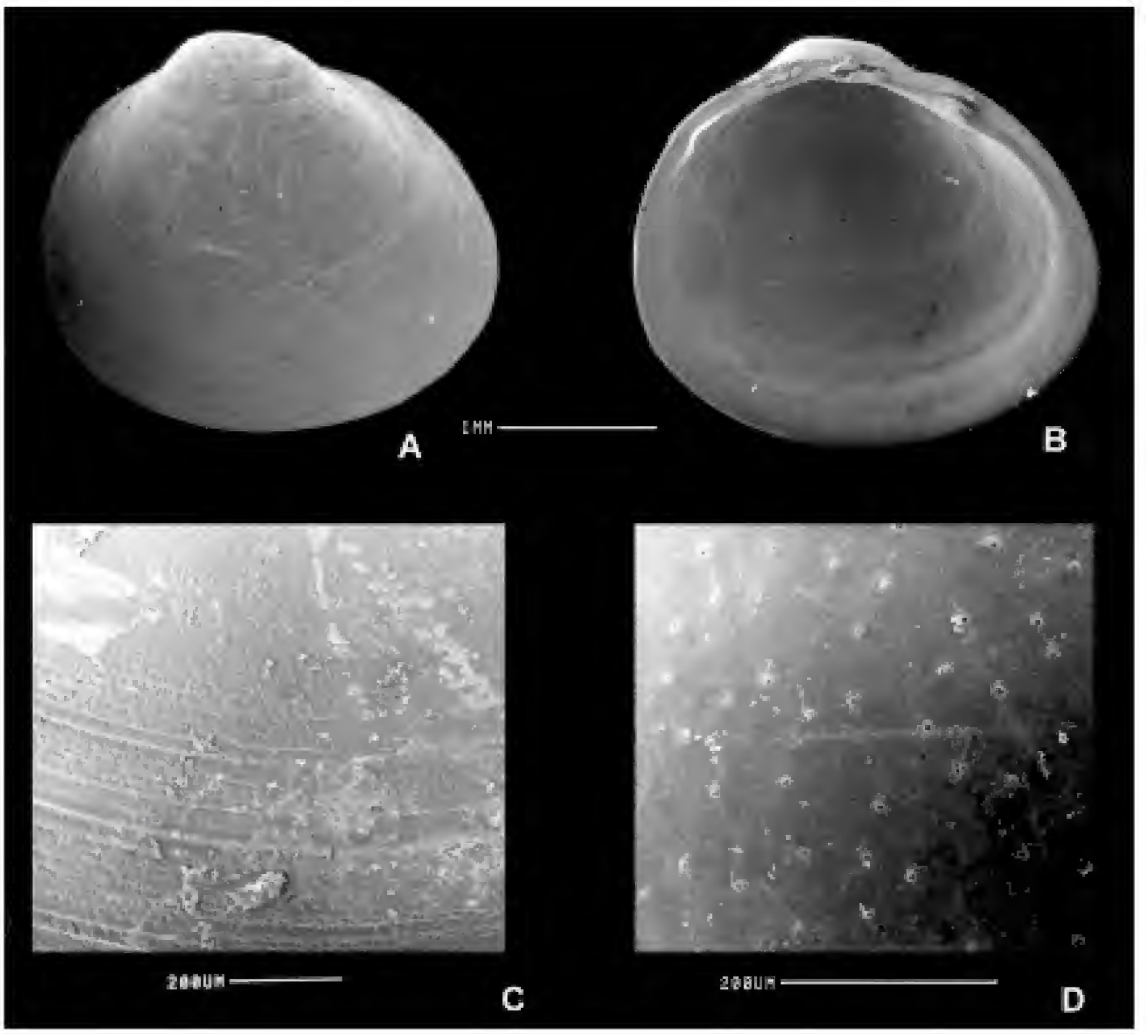


Figure 42. *Pisidium tasmanicum*, Wandle River, Tas. (AM C135192), shell: A—right valve from outside, B—left valve from inside, C—sculpture, D—internal pores.

the same localities that well agree with the original description.

This species can be distinguished from *Pisidium etheridgei* which inhabits the same lakes in the very characteristic yellow colour of the periostracum (notably another endemic species of Tasmanian lakes, *Musculium lacusedes*, has the same colour), and very flat shell with angulate, sometimes irregular (deformed) outline (see Figs. 31D,E, 45C,D). Differences in pores density, position of the outer demibranch, length of the presiphonal suture and number of muscle bundles can also separate the two species (for pores density of *P. etheridgei* and *P. fultoni* in Lake Butters $t = 3.85$, $p<0.01$.). However, *P. etheridgei* and *P. fultoni* are similar and occasional intermediate specimens combining the characters of the two species (i.e. yellow periostracum with elongate shell) have been found.

Thus, in large series, *P. fultoni* can be discriminated from *P. etheridgei* unequivocally, but identification of single specimens can be problematic.

In gill and mantle characters *P. fultoni* shows some similarity to *P. carum*. However, the peculiar sculpture of the latter has never been found in *P. fultoni*.

Pisidium (Euglesa) carum (Cotton, 1953)

Figs. 47–49

Australpera cara Cotton, 1953: 21, pl. 2, fig. 2; Cotton, 1961: 189, fig. 188.

Pisidium carum.–Kuiper, 1983: 28, figs. 55–57 (except Tasmanian localities).

Type material: LECTOTYPE SAM D14454, right valve, Brown Hill Ck, western slopes of Lofty Ranges, SA, Cotton coln. PARALECTOTYPE SAM D14454, 1 specimen, same data as holotype.

Other material examined: QUEENSLAND: 0.5 km SE of Crediton, tributary of Broken River, pool with weeds in fast flowing stream, coll. WFP, P. Colman & J.B. Burch, 29 April 1975 (AMd); tributary of Lace Ck, SW of Caboolture, 27°12'S 152°45'E, coll. WFP, WP & OG, 30 August 1982 (AM C135526w); peat bogs, Carnarvon Gorge NP, 24°50'S 147°11'E, coll. WFP & P. Colman, 29 September 1984 (AM C184152w). NEW SOUTH WALES: Molong Ck, SE of Molong, coll. WFP & AK, 15 September 1996 (AMw). VICTORIA: Loddon River at Newstead, 37°07'S 144°03'E, alt. 220

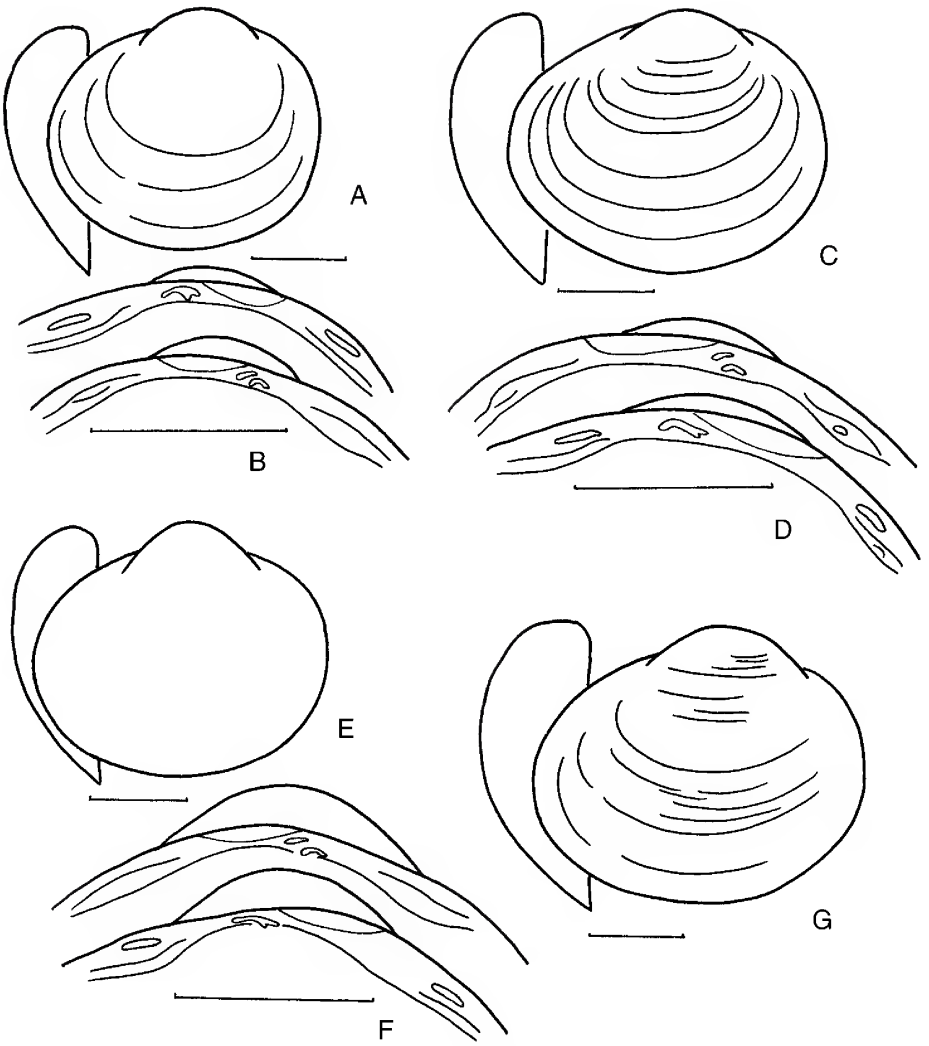


Figure 43. *Pisidium tasmanicum*, variation of shell form: A,B—Ben Lomond Rivulet, Tas. (AM, no number), left valve and hinge of the left valve; C,D—probable type lot, unlocated (TMH E112), left valve and hinge; E,F—Lake Dulverton, Tas. (SAM D19060), left valve and hinge; G—Nora River, Tas. (AM, no number), left valve. Scale bars = 1 mm.

m, coll. WFP & R. Hershler, 2 February 1984 (AM C315746w). SOUTH AUSTRALIA: Spring, Ororoo, 32°43'S 138°36'E, coll. WFP, WP & Jenkins, 7 May 1981 (AMw).

Diagnosis. Shell tetragonal or pentagonal, flat. Surface with fine regular ribs, more pronounced around umbo. Pores very dense. Hinge plate broad. Cardinal teeth strongly curved. Presiphonal mantle suture short. Inner radial mantle muscles form five to seven weak bundles. Outer demibranch relatively large, slightly shifted posteriorly.

Shell rather large (largest specimen: L 4.2, H 3.5, W/2 1.1 mm), tetragonal (trapezoid) or pentagonal, flat, thick and strong, not transparent, periostracum white or yellowish. Upper edge straight, with clear angles at extremities. Front and hind edges also straight, most extended points below horizontal median plane. Umbones relatively narrow, flat, not protruding, almost medially placed. Sculpture: clear regularly spaced ribs, more pronounced around umbones, delicate on periphery. Embryonic shell smooth. Pores abundant, their density very high (mean value 1015±462 pores per mm^2, n = 8, maximum value 1630 per mm^2).

Hinge plate broad, ligament pit short. C2 bent in smaller specimens and strongly curved in large shells, c4 hooked, placed behind c2, c3 curved, hind arm in large specimens definitely longer than front one, deeply cleft on posterior end and forming two diverging branches. Lateral teeth strong, swollen, outer lateral teeth (a3 and p3) much shorter than inner lateral teeth (a1 and p1), diverging from latter.

Anatomy (Fig. 49M–U). Mantle edge narrow. Presiphonal suture not elongate (usually 1/8 to 1/6 length of pedal slit). Inner radial muscles long, but weaker than in species observed above, forming five to seven bundles: three to four larger ones in anterior section of pedal slit and two or three smaller ones posteriorly, near presiphonal suture.

Outer demibranch relatively large, with anterior edge placed at 8th to 10th filament of inner one; mean value 9.5±0.70 (n = 10). Brood pouch formed by 5 to 8 filaments, including up to 6 embryos.

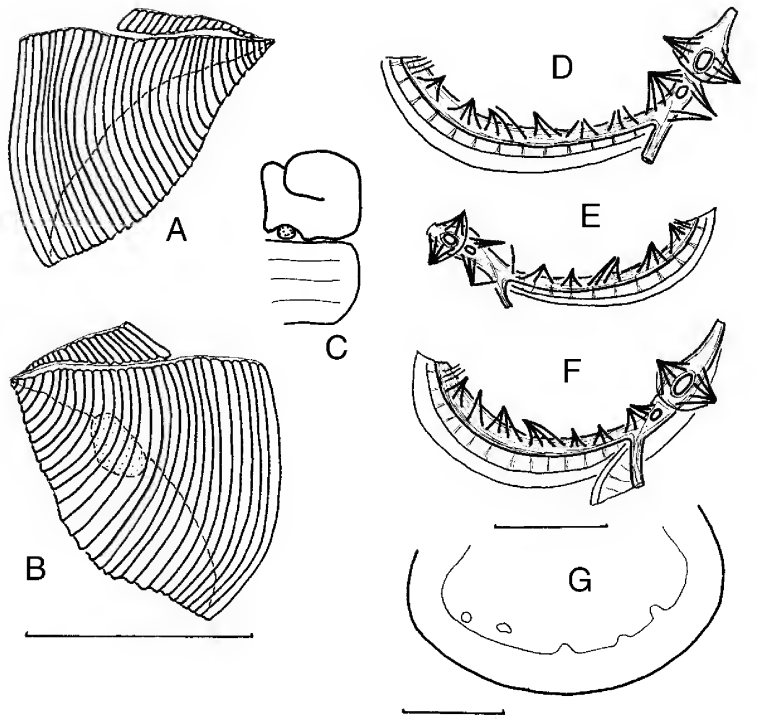


Figure 44. *Pisidium tasmanicum*, anatomy: A,B—Barwon River, Vic. (AM C317041), gills from outside; C—Wandle River, Tas. (AM C135192), nephridium dorsally; D,E—tributary of Morwell River, Vic. (AM, no number), mantle edge; F—Ben Lomond Rivulet, Tas. (AM, no number), mantle edge; G—Wandle River, Tas., mantle muscle scars. Scale bars = 1 mm.

Nephridium of closed type, with rectangular dorsal lobe.

Variability. This species is less variable than the other species in the genus. However, shells from the west slope of the Great Dividing Range in NSW have a broader hinge plate and denser pores (1420 pores per mm^2) (Fig. 48). In contrast, in Queensland specimens mean pore density was 606 per mm^2. Young specimens with relatively narrow hinge and somewhat elongate presiphonal suture, similar to *Pisidium centrale* n.sp. described below, were found in western Queensland (Carnarvon Gorge NP) (Fig. 49E,F).

Distribution (Fig. 57A). Queensland (including the northern part), western slope of the Great Dividing Range in NSW and Victoria, sporadically in South Australia; everywhere rather scarce.

Ecology. Inhabits larger streams or rivers, with a preference for sand and other hard sediments.

Remarks. Well distinguished from the other species by the shape of the shell, its solidness, peculiar sculpture and broad hinge plate. It differs from species of the *P. etheridgei* group, in having pore density, distinctive mantle characters and the position of the outer demibranch (Fig. 34). Despite some overlap in the shell morphology, differences in the quantified characters, when compared to the related taxa, are statistically significant ($p<0.05$).

Pisidium (Euglesa) ponderi n.sp.

Figs. 50–53

Pisidium tasmanicum.–Kuiper, 1983: 27 (part), figs. 59, 60.

Type material. HOLOTYPE C315642d, one valve gold coated for SEM, Norfolk Falls, Warung State Forest, 31°44'S 150°00'E, coll. IL & JW, 6 November 1985. PARATYPES C350019d&w, 3 valves gold coated for SEM & 13 complete specimens, same data as holotype.

Other material examined. NEW SOUTH WALES: Tia River above Tia Falls, Apsley Gorge NP, 31°10'S 151°51'E, coll. IL & JW, 10 November 1985 (AM C317038w); creek on SW side of Jamieson Park, Narrabeen Lagoon, Sydney, 33°43'S 151°16'E, coll. P. Colman & AK, August 1996 (IZK); Bindi Brook, NE of Braidwood, 35°07'S 150°05'E, coll. WFP& WP, 12 January 1981, det. J. Kuiper as *P. tasmanicum* (AM C126348w); Currambene Ck on Snowball Rd, 35°54'S 149°36'E, coll. WFP, 1981, det. by J. Kuiper as *P. tasmanicum* (AM 126716d); Bobundara Ck at road crossing, 29 km south of Cooma on Myalla Rd, 36°30'S 149°07'E, alt. 900 m, coll. GC, 4 November 1990, with *Pisidium etheridgei* (AM C315743w).

Diagnosis. Shell short oval or subtrigonal, convex. Surface with fine regular ribs, more pronounced around umbo. Pores very dense. Hinge plate relatively narrow. Cardinal teeth slightly bent. Presiphonal mantle suture short. Inner radial mantle muscles form five to seven weak bundles. Outer demibranch relatively large, slightly shifted posteriorly.

Table 5. Measurements (mm) of *Pisidium ponderi* n.sp.

	L	H	HH	LL	LH	LA	W/2
holotype	2.77	2.31	0.10	0.46	1.53	1.62	0.89
paratype	3.53	3.00	0.12	0.72	1.93	2.60	1.02
paratype	3.22	2.78	0.15	0.77	1.78	2.42	0.99
paratype	3.21	2.65	0.13	0.69	1.78	2.33	1.05
paratype	2.99	2.50	0.11	0.61	1.60	1.83	0.88
paratype	2.80	2.30	0.12	0.61	1.59	1.56	0.78
paratype	3.11	2.57	0.12	0.72	1.72	1.72	1.12
paratype	2.71	2.27	0.11	0.54	1.55	1.48	0.80
paratype	2.23	1.87	0.10	0.42	1.25	1.29	0.73
paratype	2.33	1.88	0.14	0.51	1.32	1.36	0.75

Shell small (Table 5, largest specimen 3.5 mm long), circular, short oval or subtrigonal, convex (some specimens inflated, almost spherical), rather solid, white or yellowish. Upper margin straight, usually with rounded angles at extremities. Back margin rounded or somewhat truncated. Front margin straight in upper section, then strongly curved, with most extended point below horizontal median plane. Umbones rather broad, protruding, almost median. Sculpture: thin regularly spaced ribs, higher and coarser around umbones. Prodissoconch smooth. Pores dense, on average 575±118 pores per mm^2 (n = 12).

Hinge plate narrow. Ligament pit rather long and narrow. Cardinal teeth: c2 bent or arched, c4 straight, placed above and behind c2, c3 curved or bent, posterior arm longer than anterior one and deeply cleft into two diverging branches. Lateral teeth rather thick and strong, but not swollen.

Anatomy. Mantle edge narrow. Presiphonal suture not elongate (usually about 1/7, in small animals 1/6–1/5 length of pedal slit). Mantle musculature of same pattern as in *P. carum*: inner radial mantle muscles long, moderately developed, forming five to seven bundles, four anterior bundles largest (Fig. 53C,D).

Anterior edge of outer demibranch placed at 8th to 10th filament of inner one (mean value 9.5±0.66, n = 12) (Fig. 53A,B). Brood pouch formed by five to six filaments, with four to six embryos.

Nephridia of closed type, dorsal lobe rectangular (Fig. 53E).

Variability. Shell size and convexity are apparently associated: smaller specimens being more convex, the smallest ones having a globose shell.

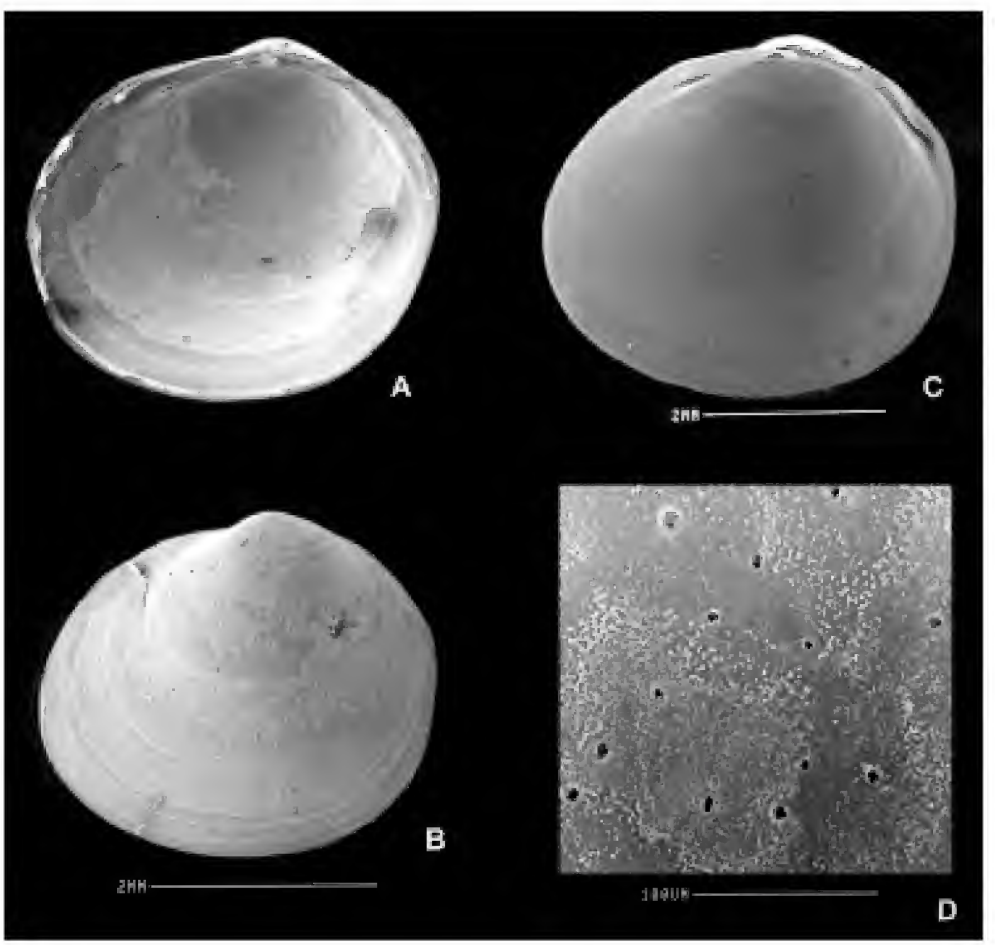


Figure 45. *Pisidium fultoni* Kuiper, shells: A,B—Lake Butters, Tas. (AM, no number), right valve from inside, left valve from outside; C,D—Lake Malbena, Tas. (AM, no number), C—right valve from inside, D—internal pores.

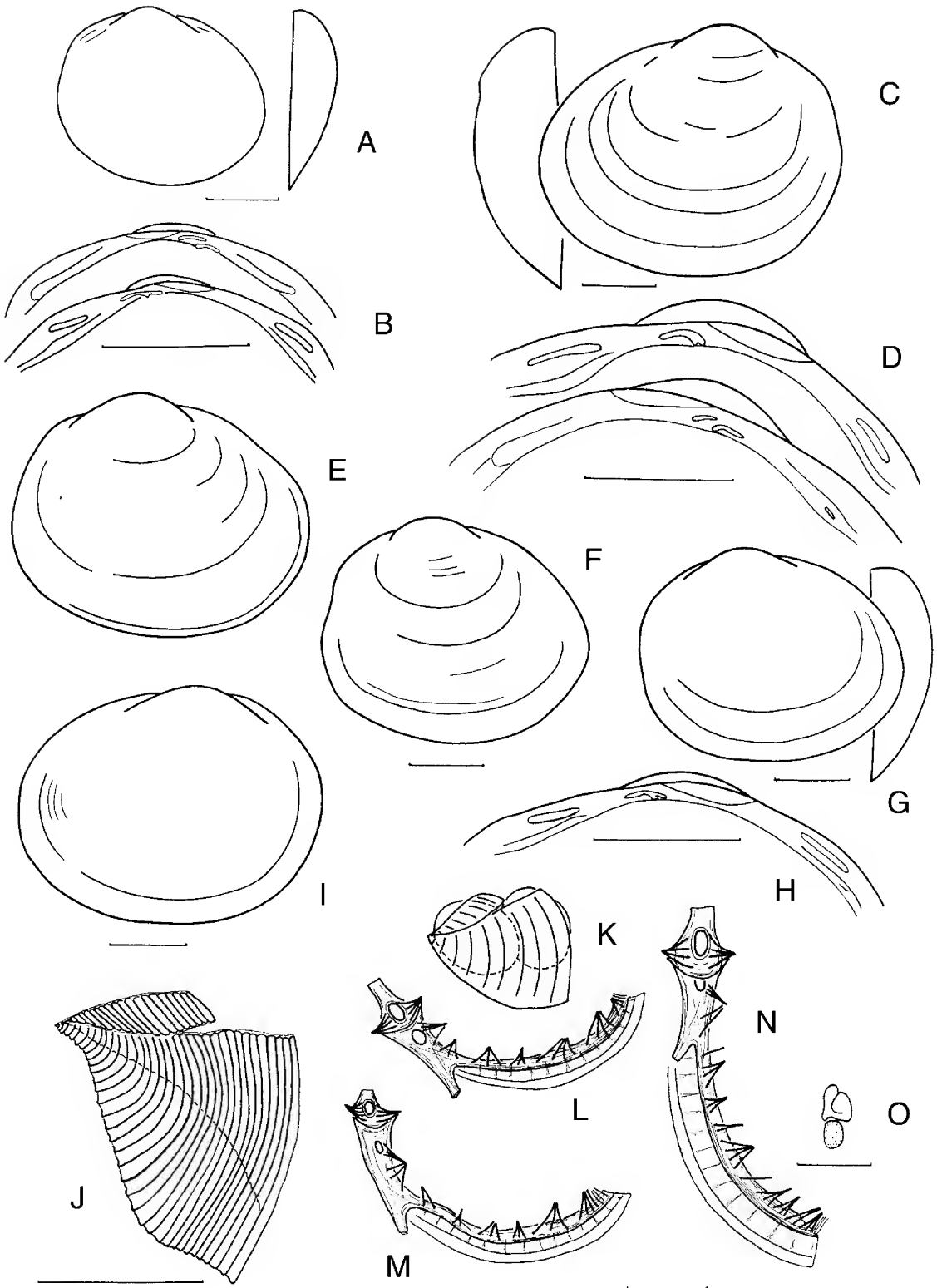


Figure 46. *Pisidium fultoni*, shells and anatomy: A,B—one of the paratypes (SMF 192865), right valve and hinge; C,D—Great Lake, Tas. (TMH E5194), large specimen, left valve and hinge; E,F—Lake Malbena, Tas. (AM, no number), variations of the shell form; G,H—Lake Olive, Tas. (AM, no number), right valve and hinge of the right valve; I—Lake Nugetena, Tas. (AM, no number), left valve; J—Lake Butters, Tas., gill from outside; K—gill with large larvae from the same locality; L,M—Lake Butters, Tas., mantle edge; N,O—Lake Malbena, Tas., N—mantle edge, O—nephrium dorsally. Scale bars = 1 mm.

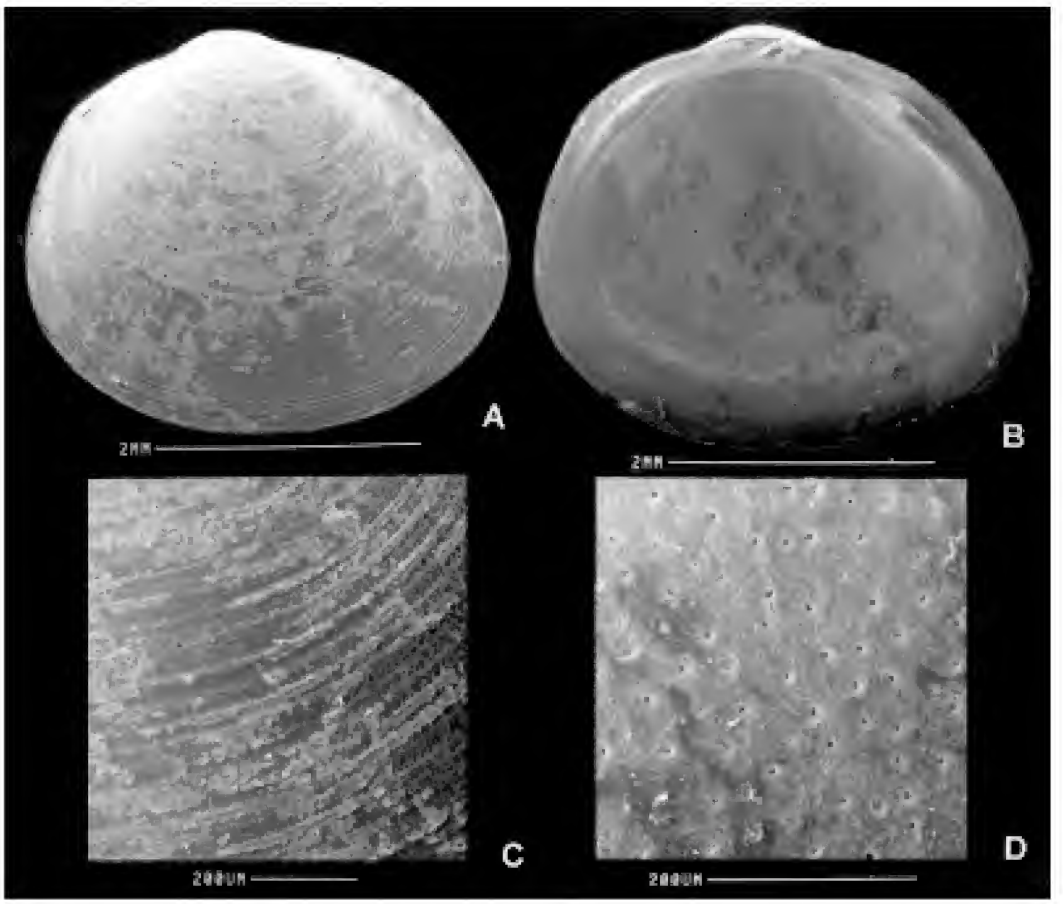


Figure 47. *Pisidium carum* (Cotton), near Caboolture, Qld (AM C135526), shell: A—right valve from outside, B—left valve from inside, C—sculpture, D—internal pores.

Distribution. The most southern part of Queensland, eastern New South Wales along the Great Dividing Range and at least one locality on the nearby coast (Fig. 57A).

Ecology. Small creeks and swamps; often associated with *P. etheridgei* or *P. hallae*.

Etymology. Named after Winston F. Ponder, Australian Museum, Sydney.

Remarks. Specimens of this species were identified by Kuiper (1983) as *Pisidium tasmanicum*. Indeed, shell outlines of these two species are rather similar. However, investigation by SEM shows that their sculpture is quite different. In the new species it is almost identical to that of *P. carum*. This affinity is also supported by the pore density, mantle musculature and the position of the outer demibranch. *Pisidium ponderi* may be distinguished from *P. carum*, by reference to its rounded, convex shell and narrower hinge plate.

Association of *P. ponderi* with *P. etheridgei* or *P. hallae* is one of the typical associations of *Pisidium* species in Australia. The most constant and reliable diagnostic character to distinguish these species is sculpture (see Figs. 55 and 115). Some other characters distinguishing *P. ponderi*, such as the rounded shell, dense porosity, short presiphonal suture and relatively large outer demibranch are also useful, but considerable individual variation should be taken into account.

Pisidium (Euglesa) centrale n.sp.

Figs. 54, 55

Type material. HOLOTYPE AM C138753d, gold coated for SEM, swamp in Stokes Ck Canyon, George Gill Range, NT, 24°22'S 131°45'E, 26 May 1983. PARATYPES AM C350021d&w, 2 valves and 16 complete specimens, same data as holotype.

Other material examined. NORTHERN TERRITORY: Reedy Ck on George Gill Range, coll. W. Horn, undated, det. by J. Kuiper as *Pisidium* sp. (AM C2148).

Diagnosis. Shell broad oval, flat. Surface with fine regular ribs, more pronounced around umbo. Pores of moderate density. Hinge plate relatively narrow. Cardinal teeth bent or arched. Presiphonal mantle suture slightly elongate. Inner radial mantle muscles form up to eight weak bundles. Outer demibranch relatively large, slightly shifted posteriorly.

Shell rather large (Table 6, maximum 4.4 mm long), broad oval, very flat, thin and fragile, subtransparent, with horn-

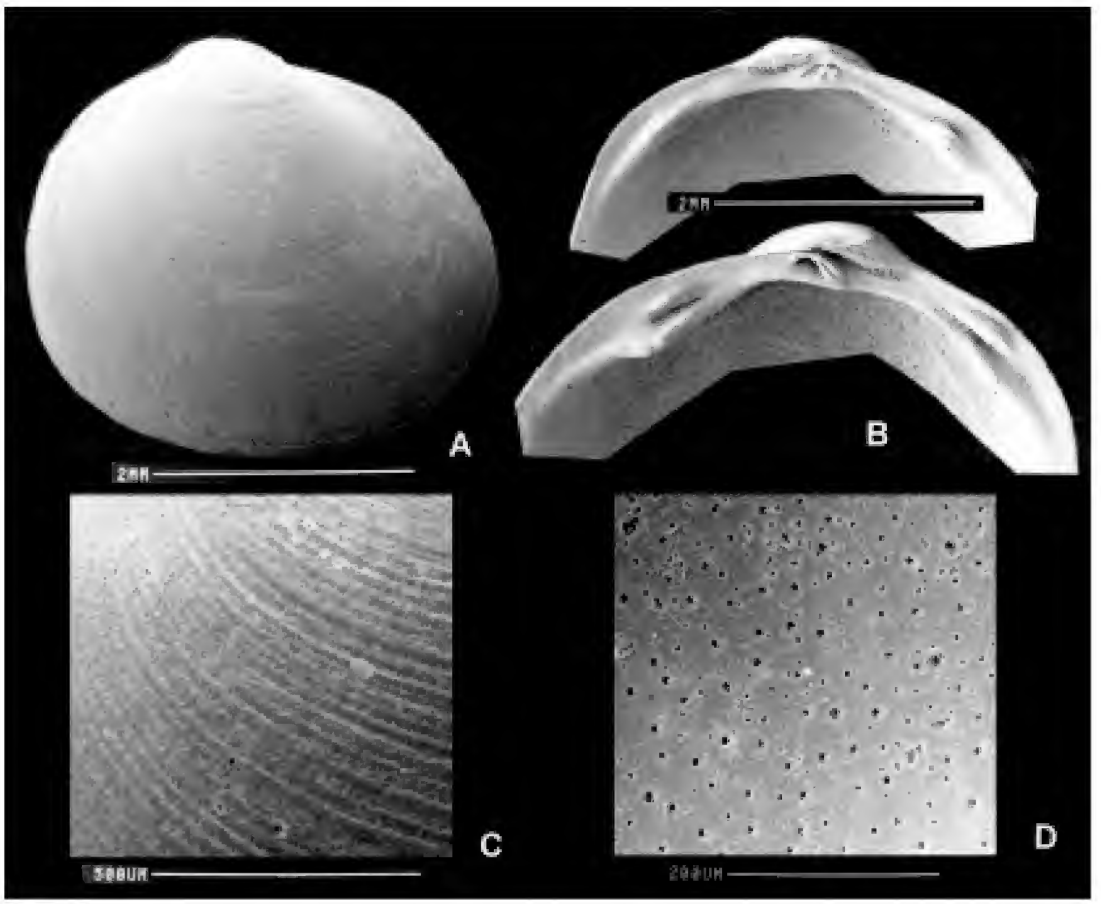


Figure 48. *Pisidium carum*, Molong Ck, NSW (AM, no number), shell: A—right valve from outside, B—left valve from inside, C—sculpture, D—internal pores.

coloured periostracum (old shells white). Upper margin long and straight, angles at its extremities rounded. Other margins evenly curved; ventral margin strongly curved. Most extended points of front and back margins are approximately at level of horizontal median plane. Umbones narrow, flat, not protruded, placed medially or slightly shifted posteriorly. Sculpture: regularly spaced concentric ribs of the same type as in *P. carum* and *P. ponderi*, several definitely higher ribs are noticeable around the umbo. Moderately porous, mean density 356±24 pores per mm^2.

Table 6. Measurements (mm) of *Pisidium centrale* n.sp.

	L	H	HH	LL	LH	LA	W/2
holotype	4.24	3.44	0.16	0.80	2.45	2.15	1.01
paratype	4.38	3.61	0.28	0.83	2.44	2.27	1.05
paratype	3.95	3.25	0.15	0.78	2.22	2.10	0.96
paratype	3.76	3.06	0.20	0.84	2.27	1.91	0.89
paratype	2.98	2.40	0.16	0.57	1.69	1.57	0.72
paratype	3.25	2.62	0.13	0.54	1.85	1.72	0.74
paratype	3.00	2.49	0.08	0.61	1.77	1.53	0.64
paratype	3.33	2.64	0.17	0.62	1.93	1.67	0.65

Hinge plate relatively narrow. Ligament pit rather long and narrow. Cardinal teeth: c2 bent or arched, c4 straight or slightly arched, c3 bent at its middle point forming an obtuse angle, its posterior arm deeply cleft, with widely diverging branches. Lateral teeth long, straight, narrow but with swollen cusps. Outer lateral teeth of right valve smaller (shorter and thinner) than inner ones.

Anatomy (Fig. 55C–E). Mantle edge narrow. Presiphonal suture slightly elongate (1/5 length of pedal slit). Inner radial muscle bundles long, anterior bundles (four to five) rather strong, posterior bundles (two to four) weakened, total number of bundles seven to eight.

Outer demibranch beginning at 10th or 11th filaments of inner one. Brood pouches of up to eight filaments and up to seven embryos.

Nephridium of closed type, with rectangular dorsal lobe.

Distribution and ecology. Known only from two creeks in the George Gill Range, Northern Territory, central Australia (Fig. 57A).

Etymology. The name refers to the central Australian distribution.

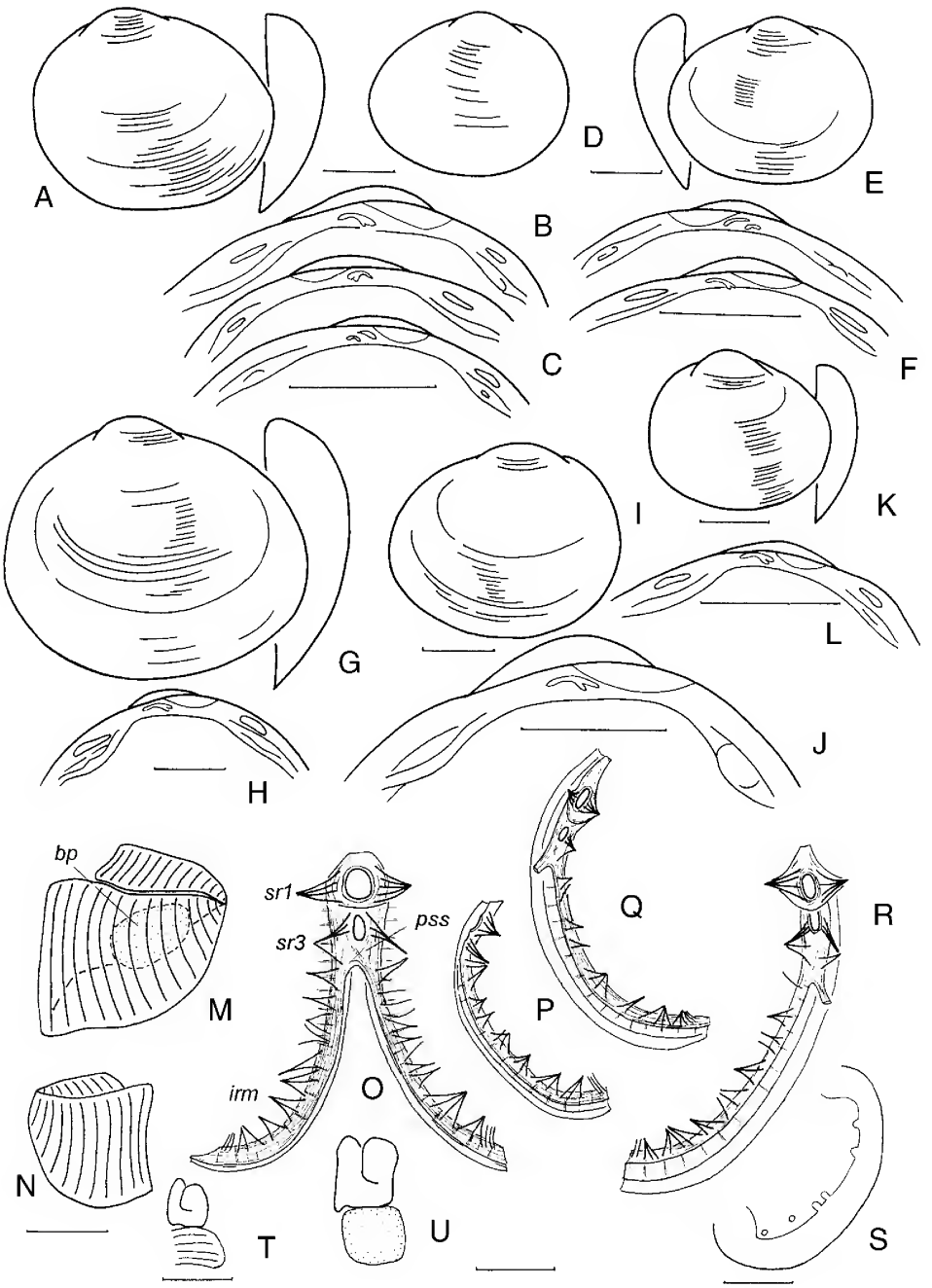


Figure 49. *Pisidium carum*, shells and anatomy: A–D—near Crediton, northern Qld (AM, no number), A—right valve, B—hinge of this valve, C—hinge with inverted cardinal and anterior lateral teeth, D—another specimen, left valve; E,F—Carnarvon Gorge NP, young specimen (AM C184152), left valve and hinge; G,H—Loddon River, Vic. (AM C315746), right valve and hinge of this valve; I,J—lectotype, Western slopes of Lofty Ranges, SA (SAM D14454), left valve and hinge of the right valve; K,L—Ororoo, SA, young specimen (AM, no number), right valve and hinge of the right valve; M,N—gills from outside, M—Loddon River, Vic., N—Caboolture, Qld (AM C135526); O–R—mantle edge, O,P—Molong Ck, NSW (AM, no number), Q,R—Loddon River, Vic.; S—muscle scars of a specimen from Caboolture, Qld; T,U—the same lot, nephridia dorsally. Scale bars = 1 mm.

Remarks. The new species is evidently related to *P. carum*, sharing with the latter a peculiar type of sculpture and pattern of mantle musculature. It is distinguished by the very flat shell (low value of convexity index notable), ovate shell outline, and the long and almost straight hinge. Differences in pore density and outer demibranch position should be confirmed on more material. In the elongate presiphonal suture of mantle the new species is similar to *P. etheridgei*.

Key to Australian sphaeriid species

Young shells of *Musculium (Sphaerinova)* species have more posteriorly placed umbones than adults and are sometimes very similar to *Pisidium* species. To distinguish the genera, study of gills and siphons is recommended. Anatomical characters also help to distinguish P. carum and *P. ponderi* from *P. etheridgei* and *P. hallae*.

1 Umbones median or slightly posterior. Adult shell more than 6.5 mm long. Both siphons with tubular extensions. Outer demibranch overlaps inner one ..... *Musculium* 2

—— Umbones placed posteriorly. Adult shell smaller (up to 5.5 mm long). Only upper siphon tubular. Outer demibranch does not overlap inner one; sometimes absent ..... *Pisidium* 8

2 Umbones very narrow, strongly protruding, prodissoconch separated by sulcus, forms a cap. Siphonal retractors strong, with their scars separated from those of adductor muscles ..... *M.* cf. *lacustre*

—— Umbones broad, prodissoconch not separated or marked by a growth break line, never forms a cap. Siphonal retractors weak, with their scars merged with those of adductor muscles 3

3 Right valve with one pair of lateral teeth (outer lateral teeth reduced) ..... *M. lacusedes*

—— Right valve with 2 pairs of lateral teeth (outer lateral teeth normally developed) 4

4 Shell rather thick and strong, not transparent (except young specimens), hinge plate relatively broad, cardinal teeth placed within hinge plate 5

—— Shell very thin and fragile, transparent. Hinge plate very narrow, cardinal teeth protrude beyond hinge plate 7

5 Shell elongate-oval, convex, umbones protruding ..... *M. quirindi*

—— Shell circular or short oval, compressed, umbones not protruding 6

6 Upper margin slightly arched, with rounded angles at extremities. Hinge plate long (cusps of lateral teeth nearer to front and back margins of shell than to umbo) ..... *M. kendricki*

—— Upper margin evenly curved, without angles. Hinge plate short, cusps of lateral teeth nearer to umbo ..... *M. tatiarae*

7 Umbones nearly median ..... *M. tasmanicum tasmanicum*

—— Umbones considerably posterior ..... *M. tasmanicum queenslandicum*

8 Ligament of enclosed type. Outer demibranch and branchial opening present ..... subgenus *Euglesa* 9

—— Ligament of other type. Outer demibranch and branchial opening absent 16

9 Shell with distinct sculpture of regularly spaced concentric ribs 10

—— Shell surface smooth or irregularly striated 12

10 Shell solid. Upper margin of shell with angles; hinge plate broad ..... *P. carum*

—— Shell fragile. Upper margin without angles. Hinge plate not broadened 11

11 Shell flat (convexity index less than 0,60), oval ..... *P. centrale*

—— Shell convex (convexity index 0.60 or more), circular ..... *P. ponderi*

12 Upper margin oblique, with definite angles, especially the posterior one. Periostracum yellow ..... *P. fultoni*

—— Upper margin parallel to the ventral one, angles rounded or not distinguished. Periostracum white, gray or brownish 13

13 Shell elongate (height/length index less than 0.78) ..... *P. hallae*

—— Shell shorter (height/length index more than 0.81) 14

14 Shell small (up to 3.5 mm), convex, umbones relatively narrow and protruding. Presiphonal suture only slightly elongate ..... *P. tasmanicum*

—— Shell larger, umbones broad, not protruding. Presiphonal suture considerably elongate 15

15 Hinge plate very narrow, cardinal teeth straight ..... *P. kosciusko*

—— Hinge plate moderately broad, cardinal teeth strongly bent or arched ..... *P. etheridgei*

16 Ligament exterior. Shell elongate, moderately convex. Sculpture—fine dense striation ..... subgenus *Afropisidium, P. aslini*

—— Ligament introverted. Shell circular, flat. Sculpture—delicate widely spaced ribs ..... subgenus *Odhneripisidium, P. australiense*

Affinities of Australian sphaeriids

A set of anatomical characters described here provides a basis for testing different phylogenetic hypotheses. However, each of the currently recognised large generic and subgeneric groups of sphaeriids represented in Australia includes non-Australian taxa or has related taxa outside Australia. Because sphaeriids from tropical regions, particularly from Southeast Asia, are poorly studied, a comprehensive phylogenetic analysis of Australian taxa is not possible. However, some preliminary suggestions on the affinities of the Australian sphaeriids are provided. The polarity of characters can be defined on the basis of phylogenetic investigations published by Dreher-Mansur & Meier-Brook (1992) and Korniushin (1998a).

A phylogenetic tree for the genera of Sphaeriidae was constructed by Dreher-Mansur & Meier-Brook (1992). According to this paper, *Musculium* and *Pisidium* are sister taxa; in turn, these two genera together form a sister taxon of *Sphaerium*. As shown above, Australian species of the genus *Musculium* included in the subgenus *Sphaerinova* (except one poorly known species identified here as *M.* cf. *lacustre*) are characterised by the considerable reduction of siphons and siphonal muscles, particularly the upper retractors of the inhalant siphon, and by the externally visible ligament. The state of the first character differs from that in the nominate subgenus of *Musculium*, and in the genus *Sphaerium*, being closer to the situation seen in the genus *Pisidium*. Thus, its apomorphic status is suggested. This suggestion is concordant with the view that reduction of siphons and some other organs is one of the principal trends in the evolution of sphaeriids (Dreher-Mansur & Meier-Brook, 1992). Phylogenetic status of the externally visible ligament is not clear, but nevertheless close relationship of the Australian species of *Musculium* seems to be well supported.

Reduction of siphonal retractors similar to that in *Musculium tasmanicum* was observed in several South American species, especially in *Musculium forbesi* (Philippi, 1869) (Korniushin, 1998b). In the African *Musculium incomitatum* (Kuiper, 1966) it is even more marked and combined with diminution of the outer demibranch and a peculiarity of the nephridium (a larger excretory sac) (Korniushin, 1995, 1998b). Some other species similar in shell characters to *Sphaerinova* are known from New Zealand (Kuiper, 1966) and India (Subba Rao, 1989), but their anatomy is unknown. Until revision of the entire genus *Musculium* is completed, it is not clear whether these similarities indicate common ancestry or convergence.

Alimov & Starobogatov (1968) assumed close relationship between *Sphaerium macgillivrayi, S. transversum* from North

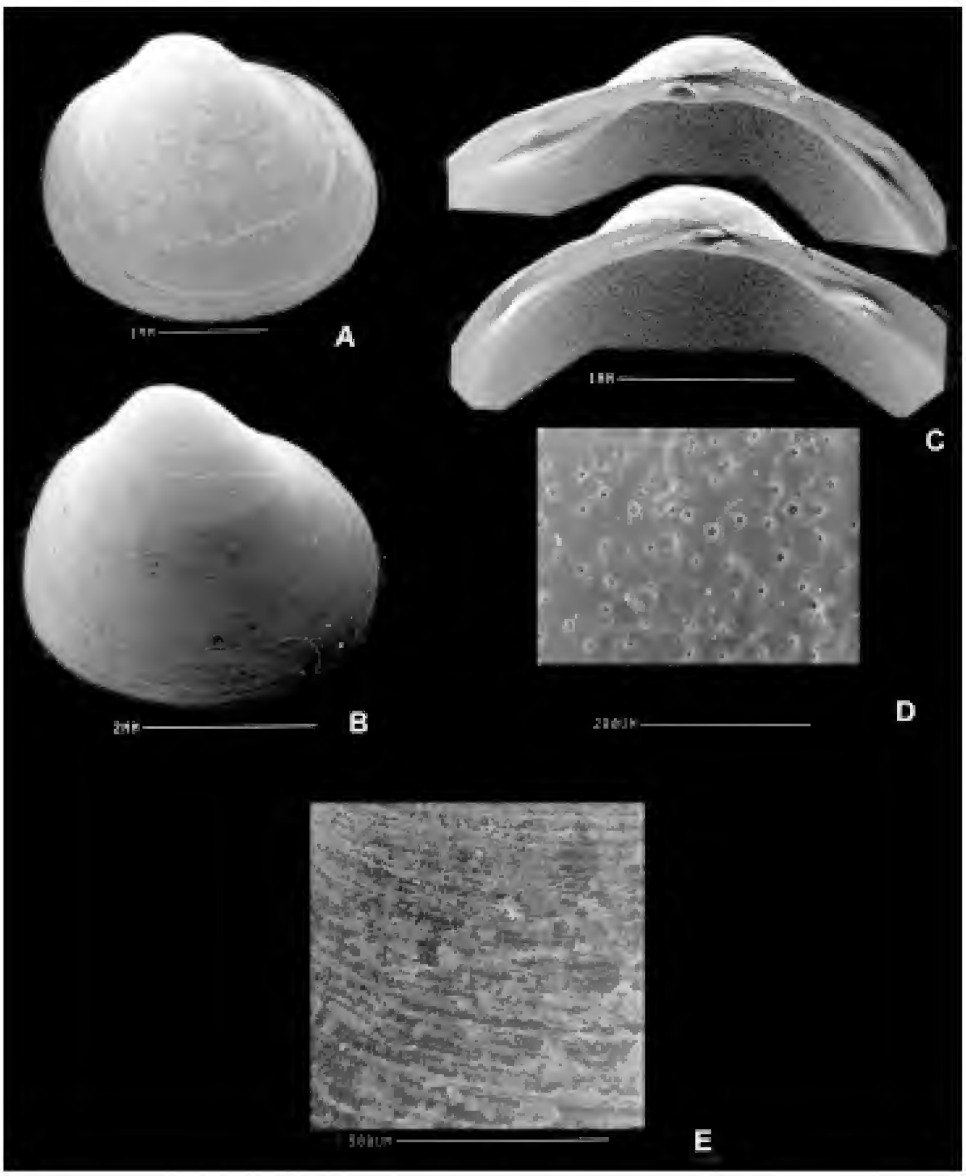


Figure 50. *Pisidium ponderi* n.sp., shells of the type specimens: A—right valve of the holotype (AM C315642) from outside, B—hinge of the paratype (AM C350019), C—right valve of the paratype, D—and pores of the paratype, E—sculpture of the paratype.

America, some African and Siberian species of *Sphaerium*. All of them were included in Iredale's (1943a) genus *Sphaerinova* and Alimov & Starobogatov attributed strong siphonal muscles and separated scars to the whole group. These views are clearly incorrect in the light of the new data on siphonal musculature of the Australian taxa.

Pisidium (Afropisidium) aslini is the most distinct Australian endemic. It differs from other consubgenors distributed in south Asia, Africa and South America in its very small size and the number of important anatomical characters (particularly in the arrangement of mantle muscles and in the shape of the nephridium). It is difficult to derive *Pisidium aslini* from any of the Asian species (for example, *P. javanum*) because of these differences and the wide geographic gap (the Australian species is distributed only in the southern part of the continent and in Tasmania). Another very peculiar species attributed to *Afropisidium* is known from New Zealand (Kuiper, 1966). Gondwanan distribution of the whole subgenus (Kuiper, 1983), and the distinct position of *P. aslini* in it, may suggest a rather ancient origin of the latter species.

In contrast, the only species of the subgenus *Odhneripisidium* found in Australia is similar to the numerous species distributed in Southeast Asia. Kuiper (1983) noted the presence of this group in Papua New Guinea, thus there is a more or less continuous distribution from the Russian Far East (Korniushin, 1996b) and Japan (Kuiper, 1983) in the north to northern Queensland in the south. The considerable species diversity of *Odhneripisidium* in east Asia suggests that Australian species may have originated from there.

Euglesa is the subgenus of *Pisidium* represented in the Australian fauna by eight species. Two major species groups are distinguished in this subgenus. The first one includes

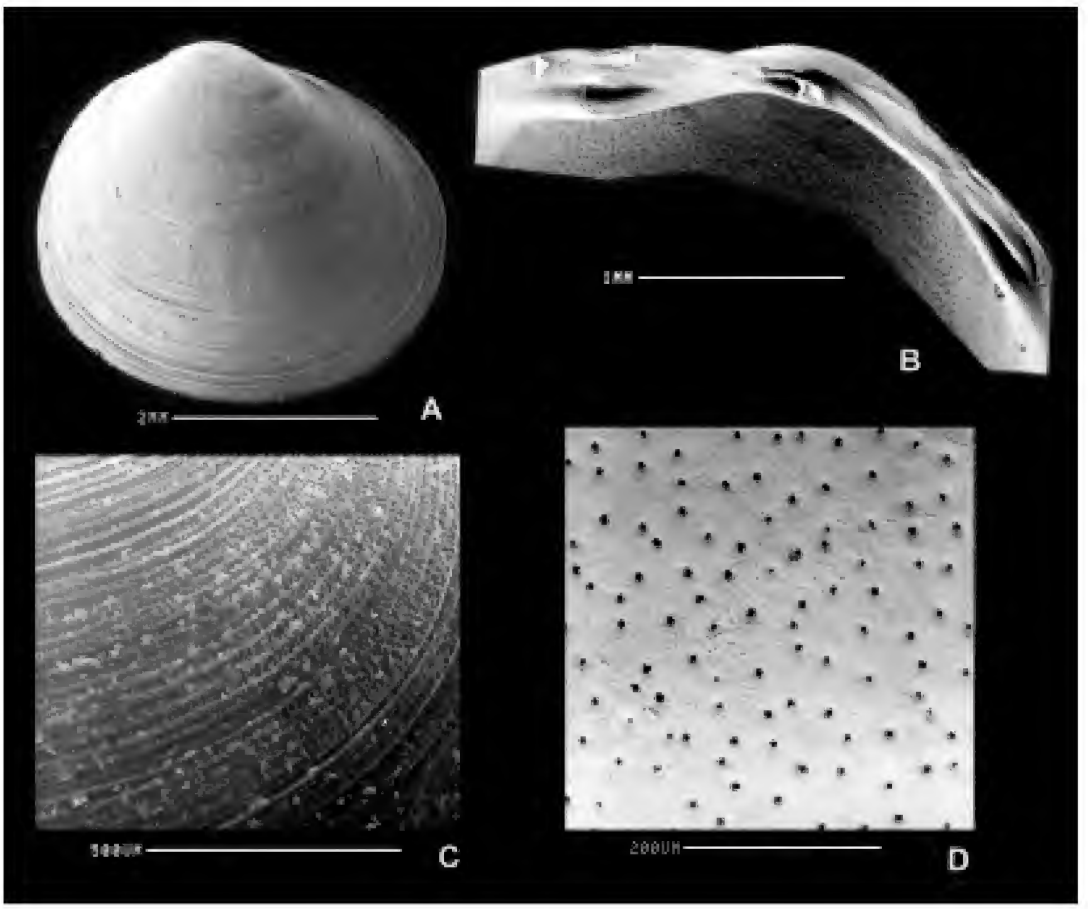


Figure 51. *Pisidium ponderi* from Bobundara Ck, NSW (AM C315743), shell: A—right valve from outside, B—hinge of this valve, C—sculpture, D—pores.

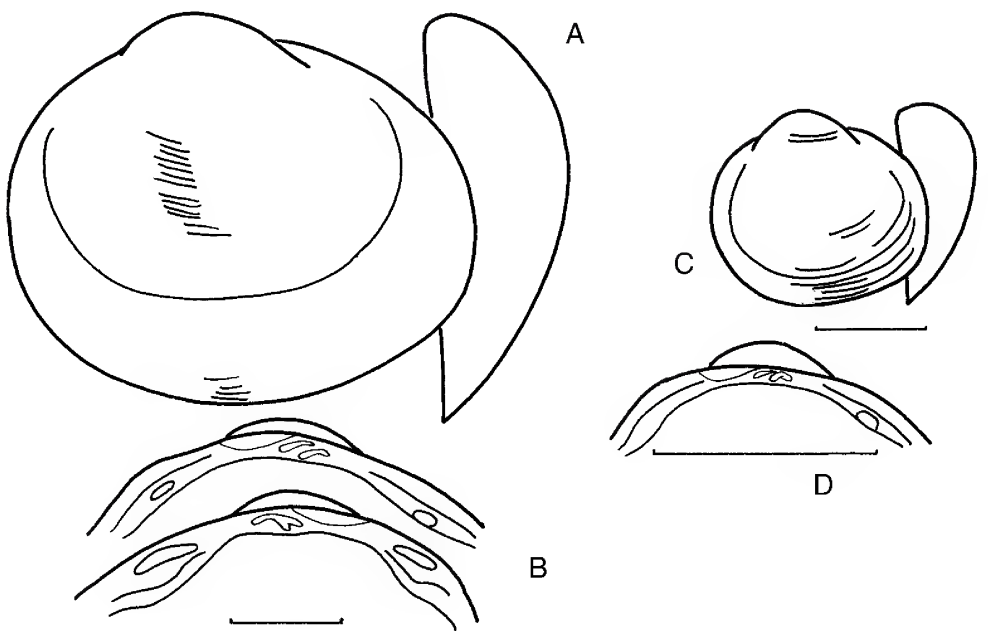


Figure 52. *Pisidium ponderi*, variability of shell form: A,B—Braidwood, NSW (AM C126348), right valve and hinge; C,D—Currambene Ck, NSW (AM C126716), right valve and hinge of the left valve. Scale bars = 1 mm.

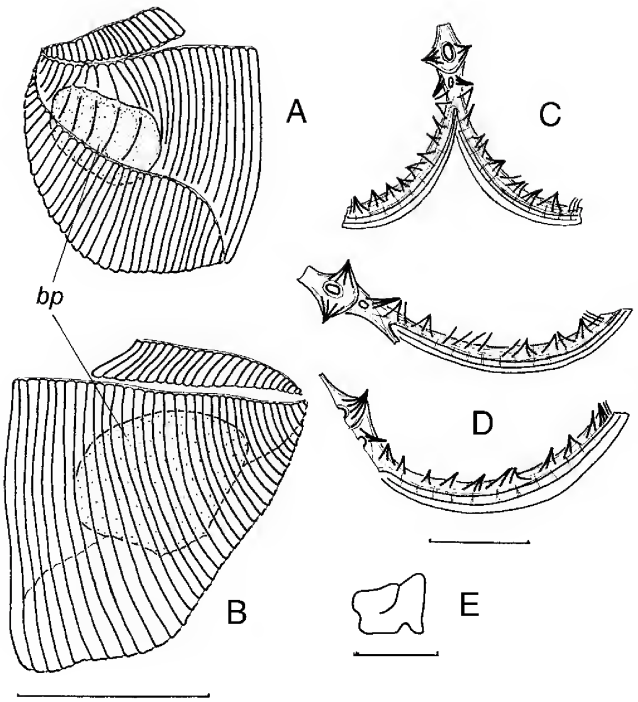


Figure 53. *Pisidium ponderi*, anatomy: A,B—gills, A—paratype (AM C350019), B—Bobundara Ck, NSW (AM C315743); C,D—mantle edge, C—paratypes, D—Braidwood, NSW (AM C126348); E—nephridium dorsally, paratype. Scale bars = 1 mm.

four species: *P. etheridgei, P. hallae, P. kosciusko* and *P. fultoni*; it is distinguished first of all in its elongate presiphonal suture which is considered an apomorphy within the genus (Korniushin, 1998a). Position of the umbo (moderately shifted posteriorly) and peculiarities of the hinge teeth (rather short lateral teeth stretched parallel to the dorsal edge of the hinge plate) are also tentative synapomorphies. Among non-Australian species, these characters are shared by *P. floresianum* found in Papua New Guinea and adjacent islands and *P. khurbaense* from the Amur River (Russian Far East). While affinities of these species to the Australian taxa are probable, this remains to be tested. The African species *P. viridarium* Kuiper, 1956 is similar to *P. etheridgei* in the shape of the shell and the arrangement of mantle muscles (Piechocki & Korniushin, 1994), but its presiphonal suture is not as elongate.

Among the species of the group discussed here *P. etheridgei, P. hallae* and *P. kosciusko* are the most similar. They are almost identical in anatomy and differ only in shell outlines and indices. *Pisidium fultoni* differs in some anatomical characters as well as in shell shape. However, ranges of variation in shell and anatomical characters in the species pairs *P. etheridgei–P. hallae, P. etheridgei–P. kosciusko*, and *P. etheridgei–P. fultoni* overlap. Species of each pair are separated geographically or by habitat (as in *P. fultoni*) and the areas of contact appear to be relatively narrow. Such a situation suggests close relationship between these species and recent speciation in the group.

Another group includes *P. carum, P. ponderi* and *P. centrale*. The close affinity of these species is supported by such tentative synapomorphies as dense pores and some reduction of mantle muscles, especially in the middle part of the mantle. The regular concentric sculpture is the other similarity between these species, but the status of this character is not clear. These patterns of sculpture and mantle musculature are shared by the South African *P. langleyanum* Melville & Ponsonby, 1891, but that species differs in its elongate presiphonal suture (Korniushin, 1995).

The relationships of *Pisidium tasmanicum* are disputable. Its affinity to the *P. carum* group is indicated by similar shell characters, but convergent development of these characters is probable. The relationship of *P. tasmanicum* with *P. etheridgei* seems to be more supportable. The short presiphonal suture found in the first species may be explained by its small size and rather short (circular) outline, and in some sympatric populations the two species are difficult to separate.

Zoogeographic regions

A summary of the distribution data (Figs. 56, 57; Table 7) makes it possible to outline several regions characterised by distinct sphaeriid faunas (Fig. 58).

A poor, but rather peculiar fauna is found in northern Queensland (one species and one subspecies are endemic for this area). The only Australian species of *Odhneripisidium* with its evident Asian affinities is the most characteristic for this area. Only one lot of sphaeriids from the coastal area in the Northern Territory is known and is considered to be consubspecific to the northern Queensland form of *M. tasmanicum*. However, sphaeriids of this area are still poorly known and the future discovery of undescribed species seems probable.

On the contrary, the fauna of the mountainous area stretching from southern Queensland to Victoria is one of the best represented in sphaeriid collections. The most characteristic species for this area are *Pisidium hallae* and *P. ponderi* (the first is scarcely represented in Victoria and Tasmania, the second is endemic). Two species, namely *Musculium quirindi* and *Pisidium kosciusko* are restricted to limited areas: an area around Tamworth and alpine lakes in the Snowy Mountains, respectively (Fig. 58). Three widely distributed species (*Musculium tasmanicum, Pisidium carum, P. etheridgei*) have mountain populations with some peculiar characters. The eastern and western slopes of the Great Divide have different faunas of sphaeriids, but the barrier is not absolute. For example, most of the localities of *P. carum* in NSW are from the western slopes, but in southern Queensland the species is represented on the eastern slopes as well. All localities of *Musculium quirindi* are from the western slopes, but *M. tasmanicum* is present on both slopes. At least three closely related species live sympatrically in the Snowy Mountains: *Pisidium etheridgei, P. hallae* and *P. kosciusko*.

The east coast has a poor sphaeriid fauna with no endemics; all the taxa recorded (three species) also being distributed along the Great Dividing Range as well.

In the vast area of the Murray-Darling basin (western plains), sphaeriids seem to be scarce, as they are poorly represented in collections. Two widely distributed species, M. tasmanicum and *P. carum*, are found in this area. There are no endemic species, but a peculiar form of *M. tasmanicum*, possibly an unnamed subspecies, is restricted

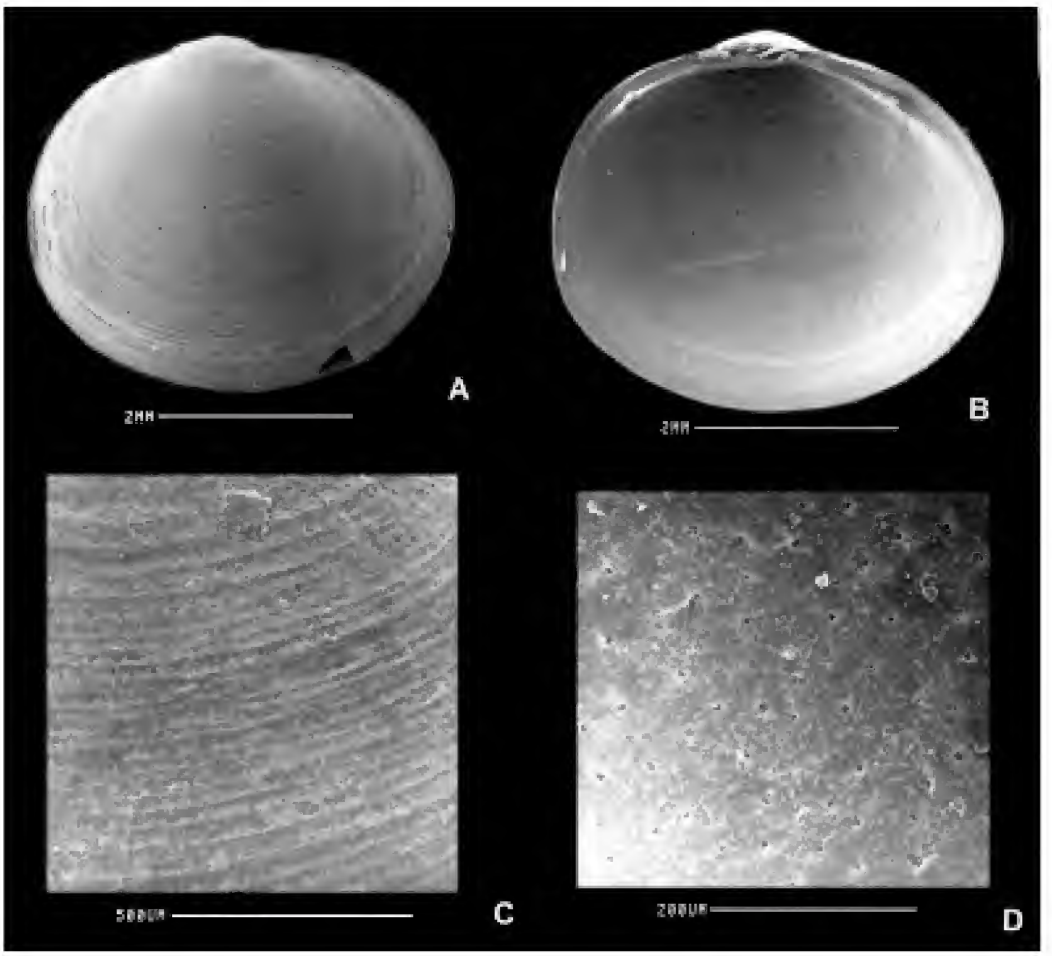


Figure 54. *Pisidium centrale* n.sp., holotype (AM C138753): A—right valve from outside, B—left valve from inside, C—sculpture, D—pores.

Table 7. Summary of the distribution data for the Australian sphaerids; 8 present, 6 absent. CA, central Australia; GD, Great Dividing Range and eastern coast; NQ, northern Queensland; NT, Northern Territory (coastal areas); SE, southeastern Australia; SW, southwestern Australia; TS, Tasmania; WP, western plains.

species	NT	NQ	GD	WP	CA	SE	TS	SW
Musculium tasmanicum s.str.	6	6	8	8	6	8	8	6
Musculium t. queenslandicum	8	8	6	6	6	6	6	6
Musculium tatiarae	6	6	6	6	6	8	8	6
Musculium lacusedes	6	6	6	6	6	6	8	6
Musculium kendicki	6	6	6	6	6	6	6	8
Musculium quirindi	6	6	8	6	6	6	6	6
Musculium cf. *lacustre*	6	6	6	6	6	8	6	6
Pisidium aslini	6	6	6	6	6	8	8	6
Pisidium australiense	6	8	6	6	6	6	6	6
Pisidium etheridgei	6	6	8	? 8	6	8	8	6
Pisidium hallae	6	6	8	6	6	6	8	6
Pisidium kosciusko	6	6	8	6	6	6	6	6
Pisidium fultoni	6	6	6	6	6	6	8	6
Pisidium tasmanicum	6	6	6	6	6	8	8	6
Pisidium carum	6	8	8	8	6	8	6	6
Pisidium ponderi	6	6	8	6	6	6	6	6
Pisidium centrale	6	6	6	6	8	6	6	6

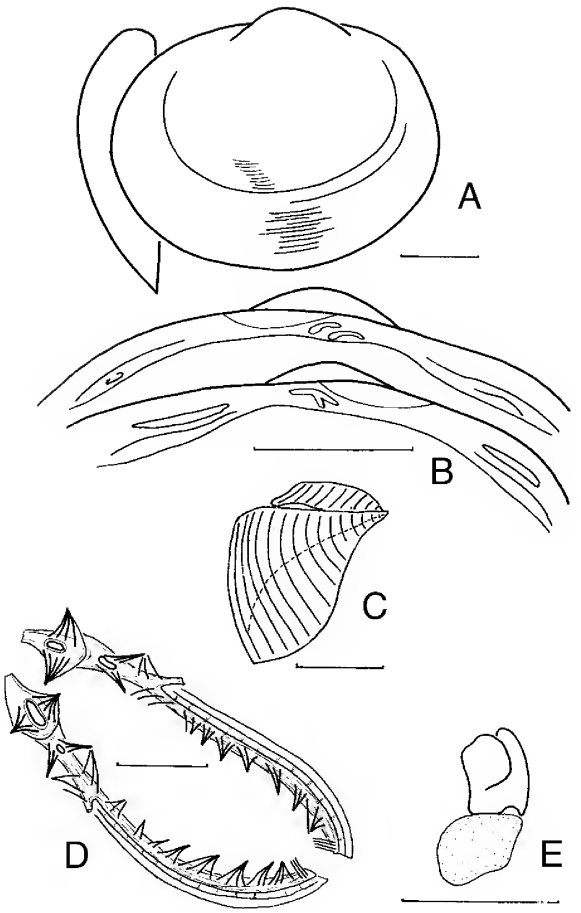


Figure 55. *Pisidium centrale*, shell and anatomy: A,B—Reedy Ck, NT (AM C2148), left valve and hinge; C–E—paratypes (AM C350021), C—gill from outside, D—mantle edge, E—nephridium dorsally. Scale bars = 1 mm.

to this region. The occurrence of another species (*Musculium tatiarae*) needs to be confirmed, and one species described from the Murray River (*M. problematicum*) is dubious. *Pisidium etheridgei* is recorded in the literature (Gabriel, 1939; B.J. Smith, 1978), but no specimens attributable to this species were seen during this study.

The southeast part of the Australian mainland is the area with the most diverse sphaeriid fauna. Its affinity to the fauna of northern Tasmania is supported by presence of *Musculium tatiarae, Pisidium aslini* and *P. tasmanicum* (the first two species are endemics to both these areas). It allows the treatment of these areas as one zoogeographic region (Fig. 58). *Pisidium aslini* is the most characteristic and possibly the most ancient element in the Australian fauna; it is presently known only from several isolated localities in Victoria and northern Tasmania. Two widely distributed species (*M. tasmanicum tasmanicum* and *P. etheridgei*) also reach Tasmania, *P. carum* is known only from the mainland. The presence of *P. hallae* in southern Victoria and Tasmania needs confirmation.

The fauna of southern part of Tasmania is poorer than that of the northern part, and most of the species are widely distributed. However, an area of endemism is located in the centre of Tasmania with two endemic species.

Only one species, the endemic *Musculium kendricki*, is known from Western Australia. Morphological study of this rather peculiar species suggests its long isolation, although some affinity to *M. tatiarae* from the southeastern Australia and Tasmania is also probable.

The other peculiar species, *P. centrale*, is known from two records in Central Australia. This extremely arid region is still poorly studied, therefore it is not clear if the mentioned species is restricted to the limited area (Fig. 58) from which it is currently known, or whether it has a wider distribution. Of interest is the lot from southwest Queensland identified as *P. carum* has some similarity to *P. centrale*.

Conclusions

The data presented here show connections of Australian sphaeriids not only to the taxa from Southeast Asia, but also to those from South Africa and South America. Among the other Australian molluscs, such distribution ranges are known for hyriid mussels (McMichael, 1967) and the heterobranch gastropod *Glacidorbis* (Meier-Brook & B.J. Smith, 1976). Such connections suggest an ancient origin of some Australian endemic taxa (*Sphaerinova, P. aslini, P. carum* and *P. etheridgei* groups) consistent in general with the point of view of Kuiper (1983). The Asian roots are evident only for the *Odhneripisidium* species found in northern Queensland; distribution of this subgenus being similar to that of the nominate subgenus of the gastropod *Gyraulus* (Planorbidae) (Meier-Brook, 1983).

Notably, Australian species form only a few anatomically distinct groups: *Sphaerinova, Afropisidium, Odhneripisidium* and two groups in *Euglesa*. The European and North American faunas are much more diverse anatomically, the former with about 20 distinct species groups (Korniushin, 1996b). At the same time, the total number of species and subspecies in Australia is rather high, with closely related species distinguished in each group. Allopatric distribution of these species and evident geographic trends in intraspecific variation suggest geographic speciation. However, this speciation was not so intensive as in small freshwater caenogastropods of the family Hydrobiidae (Ponder *et al.*, 1994). In comparison with hydrobiids, Australian sphaeriids have wider distribution ranges and less distinct morphological gaps.

The picture of the Australian sphaeriid fauna is still not complete; some regions, particularly northern Queensland and the Northern Territory, Murray Basin and Western Australia are not sufficiently well represented in collections. In addition, delimitation of some widely distributed species is not clear. Areas known to be centres of speciation—along the Great Dividing Range, as well as the central Tasmanian plateau—also need closer attention.

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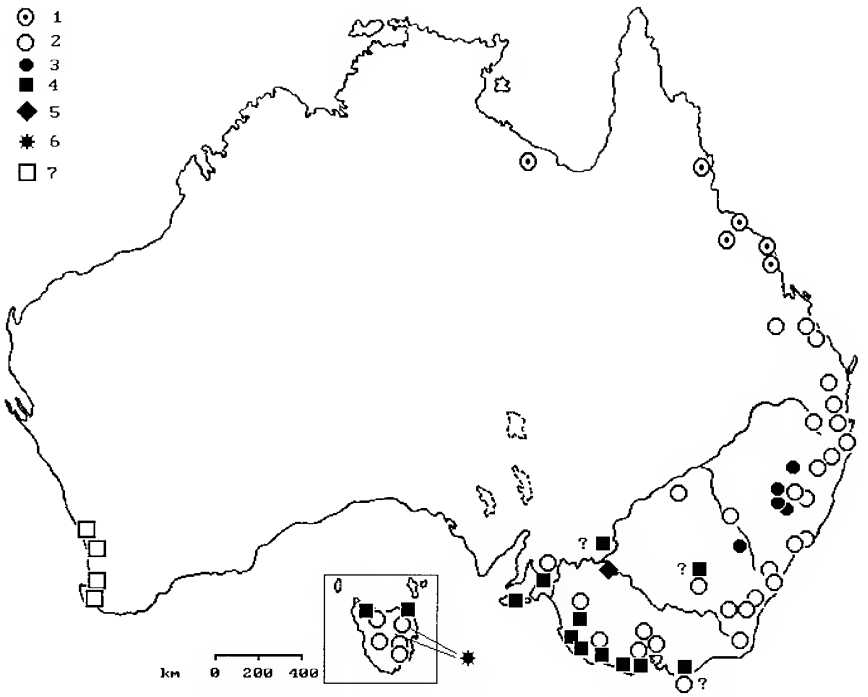

Figure 56. Distribution of *Musculium* species: 1—*Musculium tasmanicum queenslandicum*, 2—*M. t. tasmanicum*, 3—*M. quirindi*, 4—*M. tatiarae*, 5—*M. ?problematicum*, 6—*M. lacusedes*, 7—*M. kendricki*.

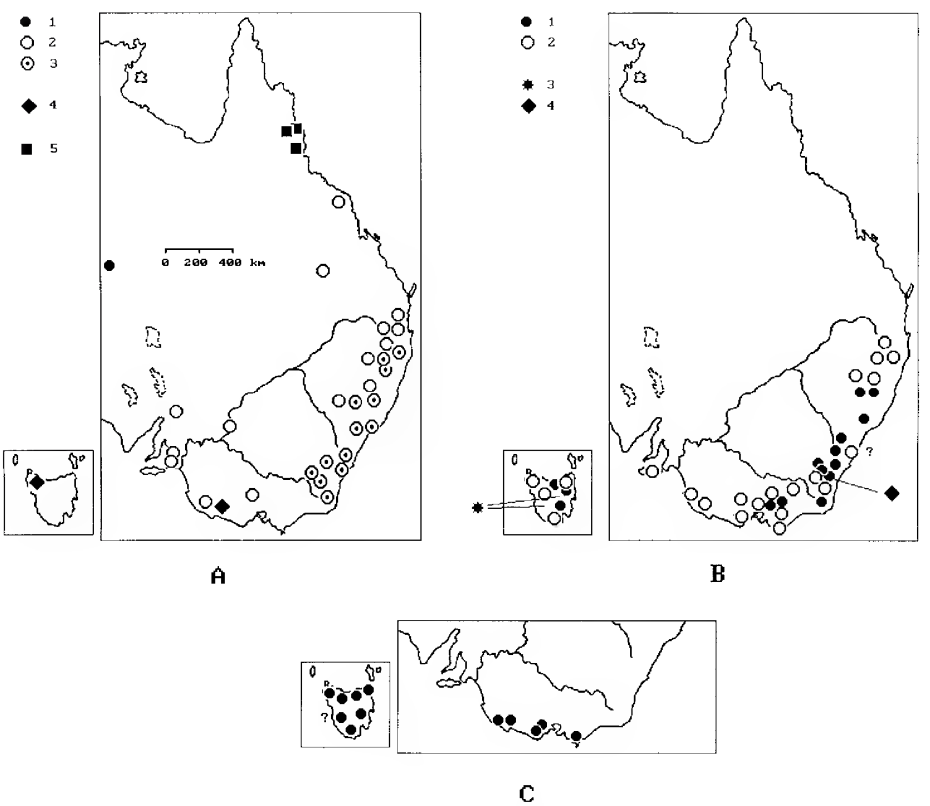

Figure 57. Distribution of *Pisidium* species: A—*P. (Euglesa) carum* (1), *P. (E.) ponderi* (2), *P. (E.) centrale* (3), *P. (Afropisidium) aslini* (4) and *P. (Odhneripisidium) queenslandicum* (5); B—species of the *P. (E.) etheridgei* group (1—*P. hallae*, 2—*P. etheridgei*, 3—*P. fultoni*, 4—*P. kosciusko*); C—*P. (E.) tasmanicum*.

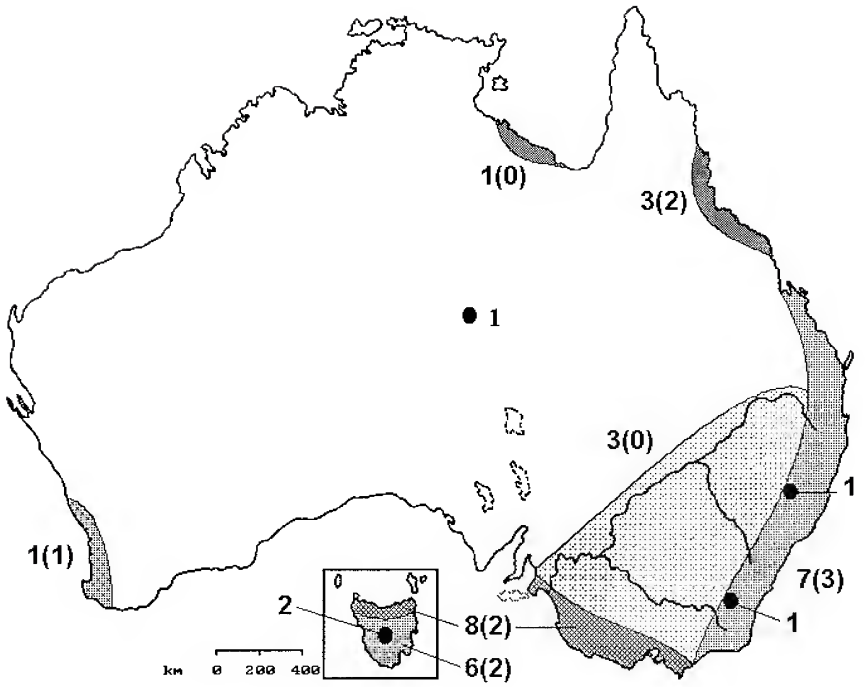

Figure 58. The regions characterised by distinct sphaeriid faunas. The total number of species and the number of endemic species (in brackets) are provided for each region. Black circles indicate the areas of local endemism, respective number of endemic species provided.

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The Braincase, Mandible and Dental Structures of the Early Devonian Lungfish *Dipnorhynchus kurikae* from Wee Jasper, New South Wales

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ABSTRACT. *Dipnorhynchus kurikae* Campbell & Barwick was described from the *Receptaculites* Limestone Member at Wee Jasper. Our new specimens include material of the braincase, the snout, the nasal capsules, the palate and the mandible which were not previously available. The new specimens give new data on the pores in the snout, the arrangement of the soft tissues in the nasal capsule, the growth of the hard tissues on the surface of the dentary, the formation of the hard surface on the palate and the prearticulars, the arrangement of sacculus and the nerves VII, IX and X in the otic region, and the interpretation of the palatoquadrate. The lateral lines on the mandible have been exposed by excavation. Thin sections show that the bone on the overgrowth of the dentary is of the same kind as occurs in the cores of the ridges on the tuberosities and marginal ridges on the palate and prearticular. A thin layer of dentine-like columns which contain no dentine tubules overlie the bony cores. This, and the mode of growth, demonstrate that the dental plates—being made of a bony core—have different patterns of deposition from tooth plates in most later Palaeozoic genera, which are made of dentine. This throws light on the way tooth plates evolved from a dipnorhynchid pattern through a speonesydrionid pattern to true tooth plates. The complex tooth plates of *Diabolepis* are considered to be independently developed. Ventrally the parasphenoid of *Dipnorhynchus kurikae* does not divide the pterygoids, but stops short at the posterior end of the pterygoids. The semicircular canals and the superior sinus of the saccular cavity are described from the well-preserved material. In comparison with *D. sussmilchi*, this species has a number of distinctive features, and is easily recognised as a separate species.

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Dipnorhynchus kurikae Campbell & Barwick, 1985, was described from two partial skull roofs, three isolated palates, two snout fragments, and two isolated mandibles. The neurocranium, the rostrum and the nasal capsules were unknown, and though the palate and lateral wings and the lower part of the neurocranium were well enough preserved, their relationships with other parts of the skull were unclear. Three new specimens of the mandible have been recovered from the type locality, including the smallest and the largest known individuals. Two new crania, one of which comes

from the type locality and the other from the same horizon about 5 km farther north, add considerably to our knowledge of the species and, though they lack roofs, they enable us to demonstrate more clearly than we could when it was first described that the species is distinct from *D. sussmilchi* (Etheridge, 1906). The oldest *Dipnorhynchus* specimens have been found in the basal part of the Cavan Bluff Limestone below the appearance of *Polygnathus dehiscens*. This suggests that they are possibly Pragian in age, making the genus the oldest or the second oldest member of the Dipnoi known at present. Morphological details of *D. kurikae* are of maximum importance because its preservation provides the best information available on the external and endocranial structures of primitive dipnoans. The new material has a section along the braincase which allows us to map out the neural features directly. One nasal capsule is fully exposed, and provides detail of the subdivision of the nasal capsule, as well as the nerves entering it.

The structure of the cheek is not known by direct observation, but reconstructions by Thomson & Campbell (1971) and (Westoll, 1989), have drawn different conclusions. Westoll concluded that all these Australian *Dipnorhynchus* are very closely comparable. Of course, this is obvious because they are congeneric; alternatively he may have been implying that a single variable species has been unnecessarily split. The present specimens add data to indicate that such a view is untenable. Westoll also interpreted the cheek of *Dipnorhynchus* with a skull that is flattened in comparison with that of *Dipnorhynchus*, and with a mandibular canal exiting from bone 4 rather than bone 5 as is normal for Devonian dipnoans.

The second partial cranium is not so well preserved, but it exposes the posterior part of the neurocranium, and a large part of the otic region. This has been known only from the holotype of *Dipnorhynchus sussmilchi*, the posterior part of which is poorly preserved, and the structures now observed permit a better reconstruction than we have had previously.

The mandibles show details of structure and the dental plates are well enough preserved to section and to examine under light microscopy and by Scanning Electron Microscopy. These sections have been compared with sections of secondary growth on the mandibles, and they are found to be closely comparable. This is of major significance for studies of the primitive dental plates in dipnoans. Similar structures are found in the tuberosities on the palate. We conclude that the animal had dental plates which had a thin layer of dentine, and were able to grow periodically by addition to bone by internal growth. The lateral lines can be excavated and show in detail their pattern. All of these features give more information on the most primitive dipnoans.

Material. The material used for this paper is as follows. SKULLS: ANU 48676, from the type locality, the base of the *Receptaculites* Limestone along a strike line of ca. 1 km around L624, of Pedder *et al.* (1970). ANU 48678 from a similar horizon, ca. 5 km north of the type locality. Rocks in this area were exposed near Cave Island during a drought. MANDIBLES: ANU 60028–60030, also from the type locality. ANU 60030 is on loan from Ian and Helen Cathles of Cookmundoon Station, Wee Jasper.

Description

The palate

Incomplete palates from four specimens are known. The most complete is ANU 48676, from which the braincase is described below (Fig. 1).

The dermopalatines are not clearly defined, but they are long and extend back to the level of the preorbital wall (Figs. 1A, 6B). Their outer edge is ridged, the posterior end having three or four rounded eminences on the ridge.

The pterygoids (Figs. 1A, 2A) are well preserved and have clear raised structures on their surfaces in some specimens, but flatter structures on others. The level of expression of these features is not related to the size of the specimens, implying a periodic reconstruction of the surfaces. The lateral margins of the pterygoids are formed of rounded ridges which, although continuous, show three or four slightly rounded eminences along their length. The most anterior ones are the most prominent, and lie against the dermopalatines—they consist of swellings which extend into the more median parts of the palate. The remainder of the lateral margin of the pterygoids extends back to the posterior end of the dental-plate, becoming narrower posteriorly. The lateral facing edges of the pterygoids have irregular denticles where lateral growth took place. In a well formed specimen, ANU 48676, the marginal ridge has a furrow against the large bosses (posterior tuberosities or blisters) that form the posterior part of the palate. White (1966: 7) referred to these elevated surfaces as raised blisters. In this paper we will refer to the elevations on the pterygoids and the prearticulars as tuberosities. On full closure these marginal ridges fit medially to the marginal ridges on the mandible. The anterior lateral tuberosities fit into the cavities behind the anterior tuberosity on the mandible.

The posterior tuberosities are variable in size and outline, but ANU 48676 (Fig. 1A) has them beautifully preserved. The anterior edge of each tuberosity has a median projection with two lobes on each side. The median projection extends forward of the others, and has a definite embayment on each side. The posterior edge of the tuberosity is broken up into irregular patches or denticles indicating that the growth took place by extension in that direction and by overgrowing these irregularities. In front of the posterior tuberosity is a large cavity in the palatal surface. *Dipnorhynchus sussmilchi* has a smaller depression which is not so well defined (Thomson & Campbell, 1971: fig. 75). The anterior median tuberosity forms a pair towards the end of the pterygoids. These tuberosities are not equal in size on the one specimen, and they fit unevenly into the median space in the mandible.

Anterior to the pterygoids but between the dermopalatines, is an open space lying anterior to the paired anterior tuberosities (Figs. 1A, 2A). In ANU 48676, the margins of the open space are rough as though a bone has fallen out. Thomson & Campbell (1971) referred to this space as being occupied by a small bone in some specimens. Such a bone is present in the specimen of *D. sussmilchi* labelled ANU 18815, but in other individuals it must have been a bone so loosely articulated with the surrounding bones that it has fallen out. With further evolution in which reduction of the dermopalatines occurs, this bone becomes isolated at the

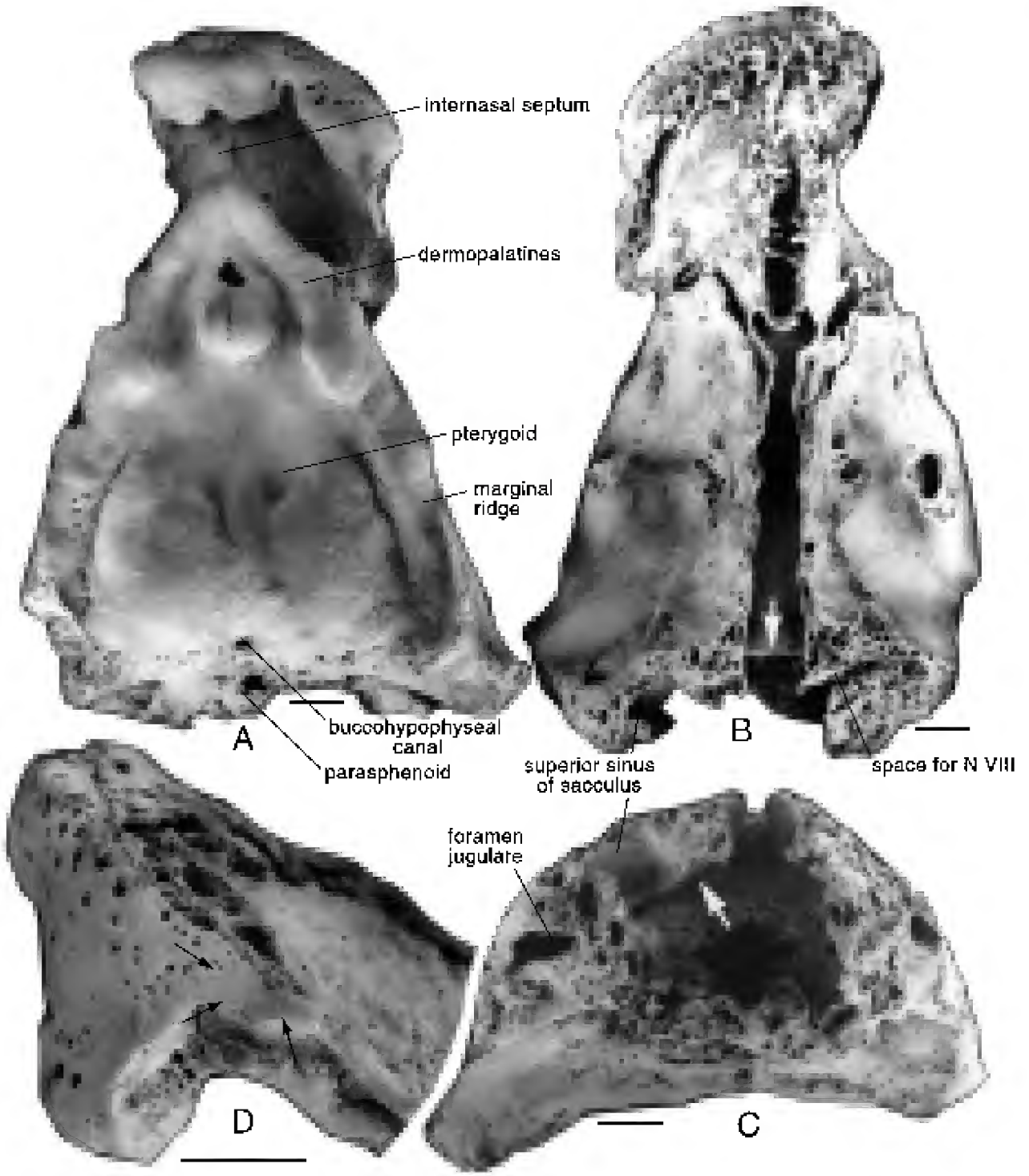

Figure 1. *Dipnorhynchus kurikae*, all parts of this figure are of ANU 48676. A,B—ventral and dorsal views of a skull from which the roof was removed during preservation. In A, note the shape of the posterior and anterior palatal tuberosities, the position of the buccohypophyseal opening, and the shape of the anterior naris. In B, note the shape of the braincase, the closely spaced neurocranial walls, the swelling on the superior sinus of the sacculus, the space for nerve VIII and the back of the endocranial wall of the braincase where it joins the notochordal cavity (white arrow). C—posterior view of the specimen. Note the end of the notochordal cavity, the position of the nerve VII on the left (white arrow), the superior sinus of the sacculus, the walls of the sacculus, and the foramen jugulare. D—view of the labial pouch and snout showing a small area of cosmine on the dermal roof. Note the large excavation for the labial pit. Scales = 10 mm.

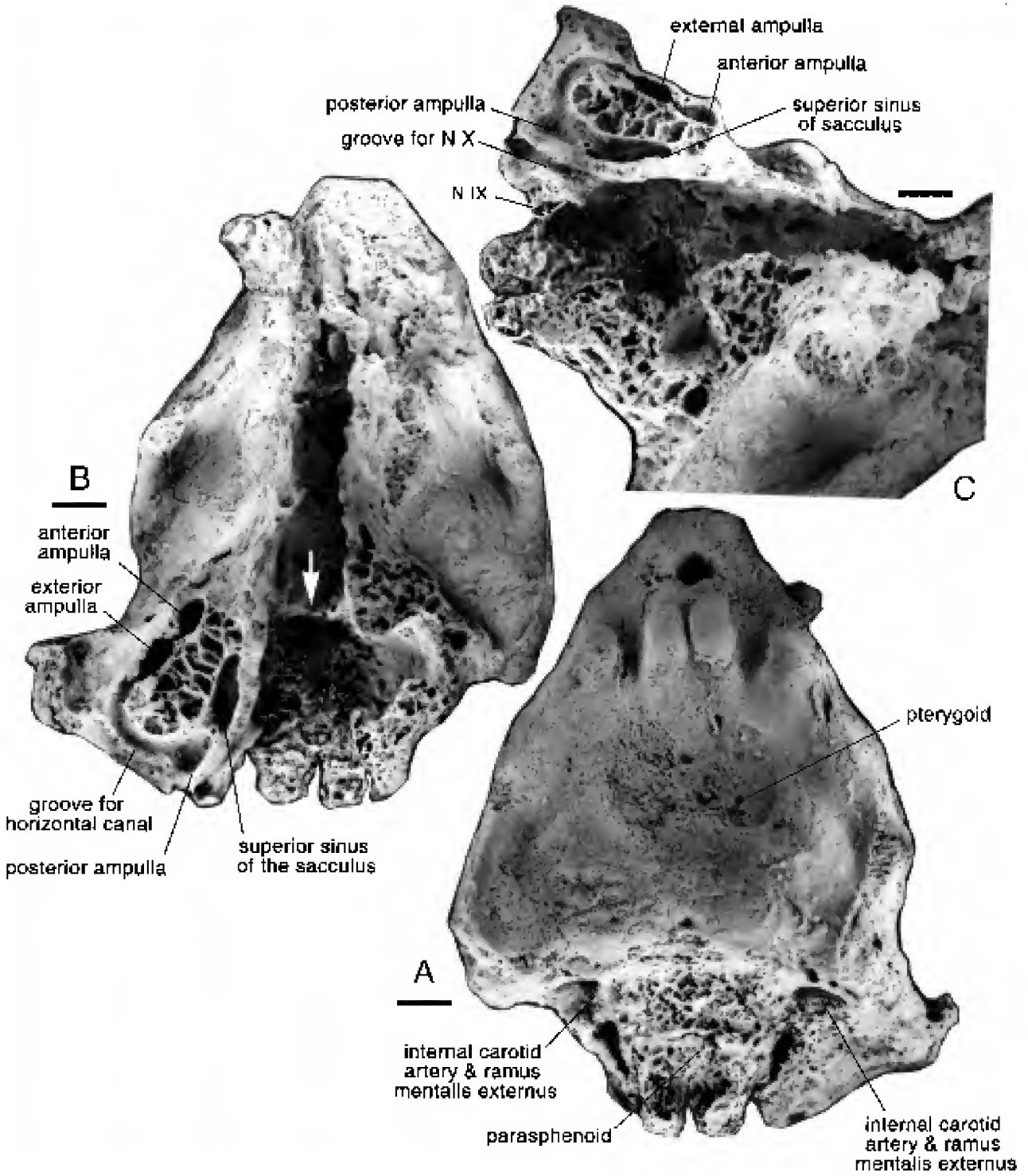

Figure 2. *Dipnorhynchus kurikae*, an isolated palate and braincase, ANU 48678. A—ventral view. Note the shapes of the tuberosities on the palate, the gross form of the parasphenoid and the position of spiracular recess. B—dorsal view, left side worn through to the level of the horizontal semicircular canal and the position of the superior sinus of the sacculus. The three ampullae of the semicircular canals well shown. Anterior edge of the notochordal cavity marked with a white arrow. See also Fig. 4A. C—dorsolateral view of the braincase. Nerves IX and X and the ampullae marked. For detail see Fig. 5. Scales = 10 mm.

front of the pterygoids (Miles, 1977: fig. 67). Although Miles (1977) refers to the isolated bone in front of the pterygoids of *Chirodipterus australis* as the vomer, we consider that the bone is not homologous with the vomers in any other group, but is a neomorphic feature in dipnoans. This is a highly significant point, as some workers consider the presence of vomers to be of significance in discussing relationships of dipnoans. For example, some workers consider that *Diabolepis* is the sister group of the Dipnoi, and it has an anterior pair of bones which are named the vomers. We see no evidence that these paired bones in *Diabolepis* (Chang, 1995: fig. 11) are the homologues of the isolated bone in dipnoans.

As was shown by Campbell & Barwick (1985: fig. 6d) cross sections of the palate show no signs of a boundary between a parasphenoid and the pterygoids on the buccal surface, but its outline is seen anterior to the buccohypophyseal tube on the dorsal surface. It was attached to the posterior end of the pterygoids, and the only way it could have increased in size was by the addition to its posterior and lateral edges. On ANU 48676 only the anterior end of the parasphenoid is preserved, but on ANU 48678 (Figs. 2A,B) most of it is present, even though the ventral surface is eroded. It rises dorsally in a sharp even curve from the palate and then turns posteriorly to make a short process. This is very similar to that of *D. sussmilchi*, which also has a median furrow that breaks through the bone in the same way. It seems to us that a thin layer of bone was present in this region, but it is not preserved. Once again, there is no similarity between the structure of the parasphenoid in these primitive dipnoans and the parasphenoids in *Diabolepis* (Chang, 1995: figs. 4, 11) which is close to that of the porolepiforms.

On the posterior wall a large recess, named the spiracular recess by Thomson & Campbell (1971), is also present in this species. This foramen was for the internal carotid artery and the ramus mentalis N VII. No matter how we interpret this opening, there is no structure like it in *Diabolepis* (Chang, 1995).

The buccohypophyseal foramen lies towards the posterior end of the palate, but its relation to the posterior end of the palatal thickening varies from specimen to specimen. It is at the end of a tube which has been described by Campbell & Barwick (1985).

The structure of the neurocranial walls

The inner perichondrium is made of continuous bone and is separated from the outer perichondrium by only 1–2 mm of endochondral bone (Fig. 1B, 3, 4). Specimens of *Holodipterus gogoensis* (Pridmore *et al.*, 1994: fig. 1) and of *Chirodipterus australis* of similar size have a greater separation between the inner and outer perichondral walls than in *D. kurikae*, and the space between them is not filled with so much vesicular tissue (Fig. 1B). The foramina for the nerves and vessels are well exposed on ANU 48676, and the canals in the bone have been removed by etching with acetic acid. It has been possible for the first time to trace the canals by inserting fine nylon line into them and observing their points of emission. An examination of this kind provides the basis for Figs. 3 and 4. The structure of the braincase wall will be discussed below, beginning at the anterior end. The description will be based on the two ANU specimens which will be referred to as required.

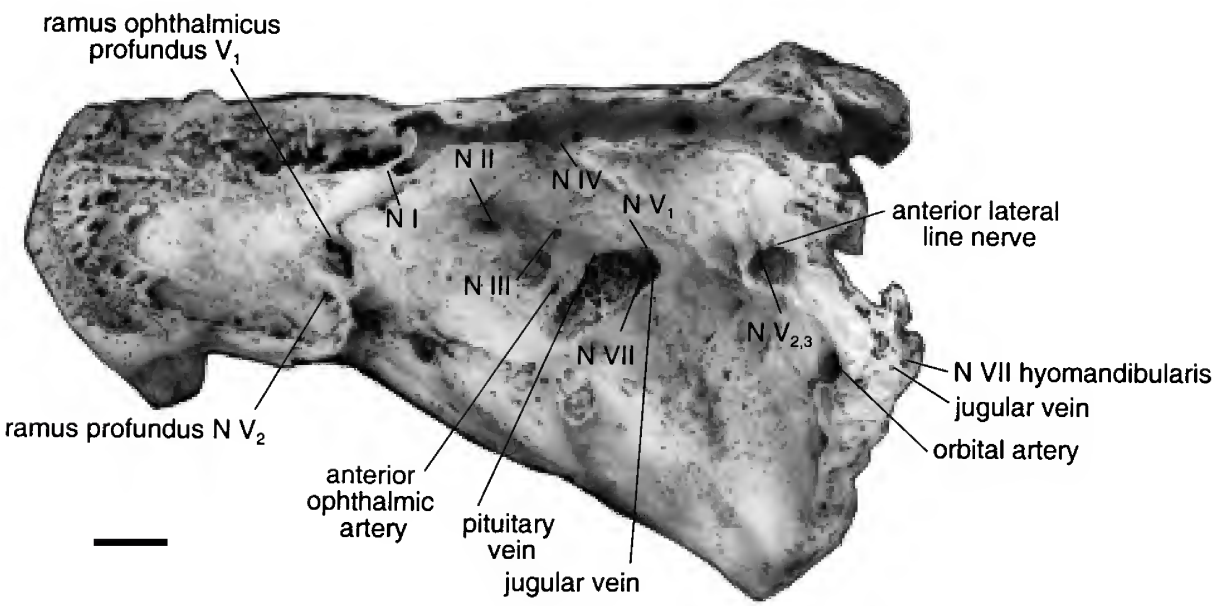

Figure 3. *Dipnorhynchus kurikae*, dorsolateral view of ANU 48676 showing the lateral features of the braincase nd the otic region. Main structures indicated and details shown on Fig. 4. Scale = 10 mm.

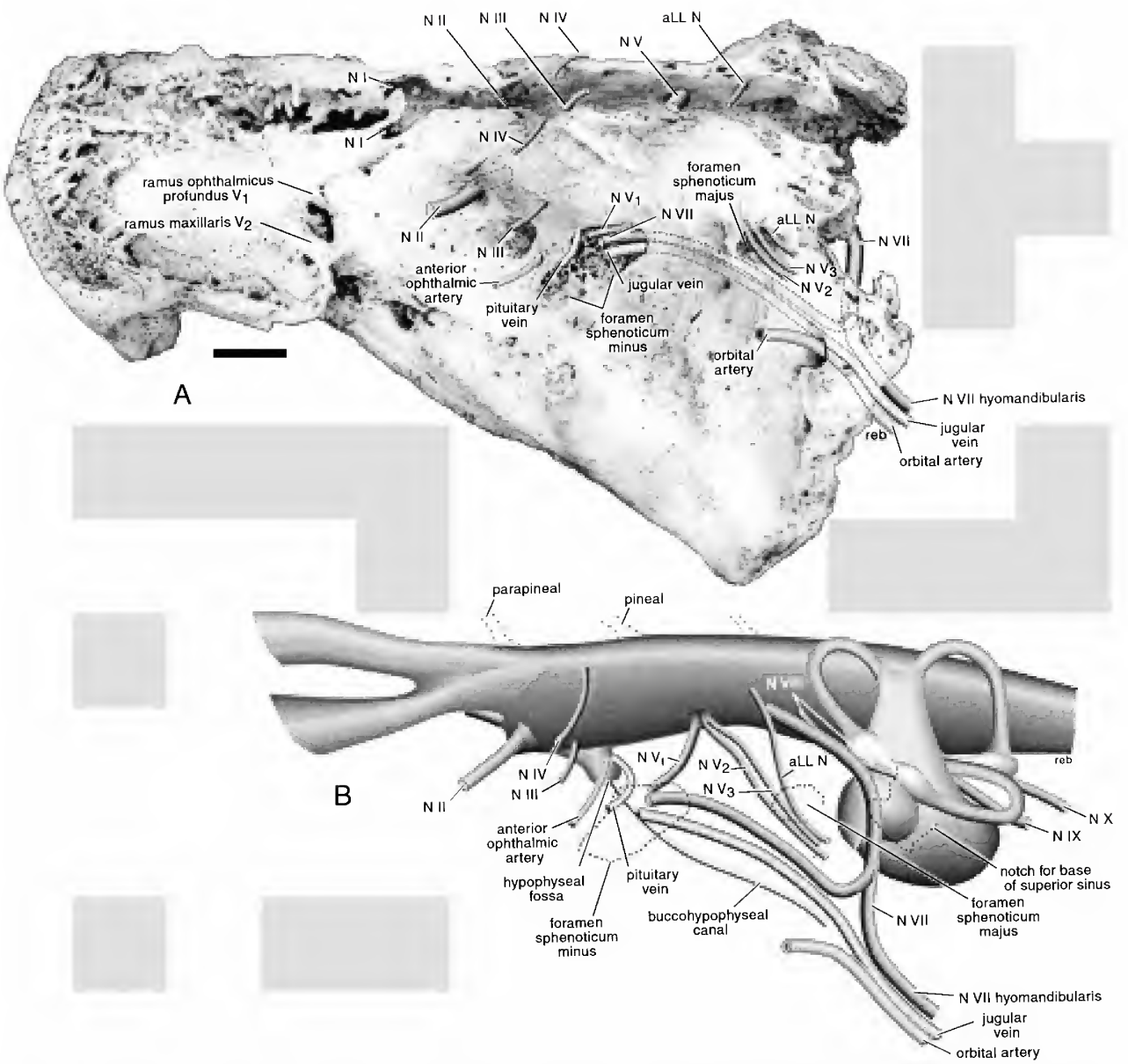

Figure 4. *Dipnorhynchus kurikae*. A—dorsolateral view of the specimen shown in Fig. 3. Nerves and vessels are indicated, with their courses shown as dotted lines where they are hidden in bone. B—reconstruction of the braincase with the dorsal surface of the braincase restored from other specimens of *D. sussmilchi*. Nerves and vessels drawn around the outline structures shown in Fig. 4A, and the otic region as in Fig. 5. The outlines of the foramen sphenoticum minus and majus, and the notch for the base of the superior sinus in Fig. 4A, shown in dotted outline. Scale = 10 mm.

Olfactory canals. The two olfactory canals separate at a point half way between the anterior end of the notochordal chamber and the tip of the snout. Each runs for 1.5–2.0 cm before opening into the nasal capsules at a junction that is marked by a slight but continuous bony rim. The walls of the olfactory canals are perforated with a number of tubules which are most common on the ventral and mesial sides, the latter joining the two sides together. Northcutt (1987: 289) commented that in *Latimeria* and *Neoceratodus* the olfactory bulbs are pedunculated, and considered that this is the primitive condition for lungfishes. This is undoubtedly correct, because all Gogo lungfishes and as well as *Dipnorhynchus* and *Speonesydrion* specimens are pedunculated. In other words, the best known Devonian species in which the snout region is well known have pedunculated olfactory regions. This is correlated with their expanded snouts containing a large number of tubuli overlying the large olfactory bulbs.

Telencephalon. As we have indicated for *D. sussmilchi* (Campbell & Barwick, 1982: fig. 25a), the floor of the telencephalon drops slightly to the rear of, and also constricts laterally, posterior to the ends of the olfactory canals (Figs. 1B, 4B). Northcutt (1987: 281) commented that in living dipnoans there is a distinctly expanded floor on the telencephalon. In dipnorhynchids any expansion of the floor of the braincase is barely perceptible. Similar comments can be made about the floor of the telencephalon in the Gogo dipnoans, and presumably this is a feature of primitive dipnoans.

A shallow depression, which is too small to photograph in such a secluded position, lies on each side of the midline in the floor of the telencephalon of *D. kurikae*. At the anterior end of each groove is a foramen, and this passes anterolaterally presumably into a tube. We have not been able to see where it emerges. Of particular interest is the entry into the right foramen by four small holes; but on the left a single perforation is present. The function of these structures remains unknown.

The dorsal surface of the telencephalon is not preserved in either specimen. However the shape of the lateral and anterior walls indicates that it was raised above the level of the more posterior parts of the braincase. We cannot determine the extent to which it was divided medially.

Diencephalon. Behind the telencephalon the walls of the diencephalon swell slightly laterally, and ventrally they drop to a point where the base of the foramen for the *opticus* N II makes its exit (Fig. 4). The optic nerve passes from the braincase via a bone-lined tube and an external foramen 5 mm in diameter and oriented mainly anterolaterally, but also a little ventrally. This is similar to the orientation shown by Campbell & Barwick (1983) but unlike that shown by Thomson & Campbell (1971: fig. 32) for *D. sussmilchi*. The optic foramen lies immediately behind the point where the preorbital wall meets the lateral wall of the braincase.

In extant dipnoans the *opticus* N II passes out dorsal to the base of the braincase, and generally it is smaller than that of *Dipnorhynchus*. In *Chirodipterus* and *Holodipterus* the *opticus* canal emerges from the base of the braincase, though in both these genera its point of exit is further forward than in *Dipnorhynchus*. The position of the nerve in these Devonian forms indicates that they display the primitive condition for dipnoans. In *Diabolepis*, the nerve II is situated in a forward position, and the nasal capsule forward of it is also short (Chang, 1995: figs. 5, 11). This interpretation is supported by the position of the orbit as shown by Chang (1995: fig. 2). Other differences between *Diabolepis* and dipnoans, such as the massive differences in the posterior of the skull, are dealt with in a paper that we have submitted for publication.

Behind the *opticus* nerve foramina, the floor of the braincase rises slightly to form the front edge of a commodious hypophyseal cavity. In this rise is a deep median groove that runs posteroventrally down into the hypophyseal pouch. The pouch swells laterally and posteriorly. The pituitary vein passes out laterally and slightly posteriorly within this pouch, and emerges into a large cavity (the *foramen sphenoticum minus*) in the lateral wall of the braincase medial to the conical palatal process (Fig. 4). The jugular vein runs from a posterior position and opens through the *foramen sphenoticum minus* slightly behind the pituitary vein. The anterior ophthalmic artery passes anteroventrally to the pituitary vein and opens low down on the lateral wall of the braincase just dorsal to the palate. The external opening for this artery is clearly visible on both sides of the specimen, but its internal opening is concealed. Presumably the internal carotid enters the posterior swelling though we have not been able to establish this point. Posteroventrally the hypophyseal pouch passes down into a long narrow buccohypophyseal canal, that opens into the mouth almost at the posterior end of the pterygoid dental plate.

Internally within the braincase, *oculomotorius* N III, is situated 2–3 mm above the anterior wall of the pituitary hypophysis. It leaves the braincase through a foramen that is only 1 mm in diameter, and passes ventrolaterally into the orbital chamber, opening about 7 mm posterior to the optic foramen.

As usual, the *trochlearis* N IV is situated high on the wall of the braincase, and in this specimen is represented on each side by a notch on the upper edge of each side of the neurocranium (Figs. 3, 4). With the palate held horizontally, this foramen is slightly anterior to a line dorsal to foramen for *oculomotorius* N III. It is oriented anterolaterally from the inside outwards.

Mesencephalon and metencephalon. Behind the hypophyseal foramen, the floor of the braincase is almost horizontal except for a broad slight median ridge along its length. The foramen for the moderately large *trigeminus* N V lies well down on the wall, and leaves the braincase about 12 mm behind the hypophyseal pouch. It is entered by a short groove which starts anteriorly. Within a couple of millimetres after leaving the inner perichondrium the tube splits; a thin tube that carried the *profundus* V_1, being directed forwards and downwards to open through the external neurocranial wall in the *foramen sphenoticum minus* on the left side of the specimen (Fig. 4B), but through a small foramen behind that structure on the right side. This nerve is in an appropriate position to run through the floor of the orbital cavity, and thence forwards to the sensory region of the snout. A second much larger tube runs posterolaterally to open through the *foramen sphenoticum majus* (Fig. 4A,B). This carried both V_2 and V_3, which serve the maxillary and mandibular rami.

On the internal surface of the braincase, dorsal to the foramen for *trigeminus* N V, a shallow groove runs upwards, but the specimen does not show any foramen at its top. This, presumably, is the result of erosion of the top of the braincase through weathering.

The wall of the *sphenoticum minus* is a coarse open structure (Figs. 3, 4A), rather than being a continuous layer. Immediately in front of the ventral edge of this structure is a small opening for the anterior ophthalmic artery, described above. Between this foramen and around the *opticus* N II foramen, the wall of the external endocranium is depressed and crinkled. A similar feature is found on some specimens of *D. sussmilchi*.

Examination of the structure of extant dipnoans *Neoceratodus* and *Protopterus* (Northcutt, 1987) shows that the *facialis* N VII and the *accousticus* N VIII leave the wall

of the braincase close behind nerve V; in addition, a branch of the anterior lateral line nerve passes out dorsal to nerves VII and VIII. The two new specimens of *D. kurikae* do not show any exits close behind nerve V, and the interpretation of the existing foramina have to be understood in terms of general principles. We reached the following conclusions.

In the inner perichondrium about 7–8 mm posterodorsal to the *trigeminus* N V foramen, is a vertically elongated foramen which runs laterally into a foramen in the top of the *foramen sphenoticum majus* on the left side, and to a small foramen dorsal to the same position on the right side. This structure is in an ideal position for the *anterior lateral line* nerve (Fig. 4B). Its position can be compared with that of *Neoceratodus, Protopterus* and *Latimeria* as illustrated by Northcutt (1987).

In the internal wall immediately below the above foramen, a shallow but wide groove runs into the front wall of the utriculus, and then runs posterolaterally into the thick neurocranial wall. Within the wall the tube splits into two, the dorsal one of these emerges in the dorsal extremity of the *foramen sphenoticum minus*, and probably carried the *superficialis ophthalmicus* N VII. The ventral one enters a long tube that runs postero-ventrolaterally to open through the *foramen prooticum basicraniale* along with the jugular vein. It must therefore be the *hyomandibularis* N VII.

Posterior to where the *facialis* N VII leaves the braincase, the walls expand laterally to form the inner face of the otic region. At the anterodorsal end of this expansion, incomplete gaps in the specimen show where nerves open out of the braincase and pass laterally through the thick lateral walls. This must have been for the nerve *accousticus* N VIII. Its course is not preserved but it must have turned into the otic region after a short distance. We assume that the brain stem maintained a linear course through this region, and we have so represented it on Fig. 4B.

The walls of the braincase turn downwards in front of the otic region, and the anterior end of the notochordal chamber penetrates this wall for about 3–4 mm. This puts the end of the notochordal chamber anterior to the level from which the nerve *accousticus* N VIII passes out.

The second specimen, ANU 48678, shows the otic region moderately clearly, except that the vertical semicircular canals are missing. Figure 5A shows the specimen with the outlines of the canals and the otic region drawn onto it, and Figs. 5B and 5C are reconstructions of the soft tissues inferred from it. The right side of the specimen has been weathered, exposing the internal structure of same. The left side has been not so deeply weathered but exposes the horizontal part of the semicircular canals. This gives sufficient information on the general structure of the region to be able to reconstruct the overall pattern.

The posterior part of the notochordal chamber has also been lost allowing observation of the sacculus, the utriculus, and the superior sinus. In addition this specimen shows the position of nerves N VII to N X more clearly than any other Early Devonian form. The utriculus is large and extends across the anterior face anterodorsally to the terminus of the notochord, and it is crossed by the *facialis* N VII as has been described above. The *accousticus* N VIII is dealt with in the section below dealing with the semicircular canals.

Nerve *glossopharangeus* N IX is known only from its exit from the posterior part of the sacculus, which is its standard position on Devonian dipnoans. It passes out in a lateral direction.

The passage of nerve *vagus* N X is preserved as a groove passing below the posterior part of the superior sinus of the saccular cavity, and then parallel with the ventral edge of the ampulla for the posterior semicircular canal. It passes out of the bone in a posterolateral direction.

The horizontal semicircular canal is not evenly curved, its external edge being almost straight. Its external ampulla lies well behind the anterior end of a transverse line through the superior sinus of the saccular cavity. Below the external ampulla it turns ventrally into the sacculus. Posteriorly the horizontal semicircular canal maintains its width throughout its length, and passes into the posterior end of the superior sinus of the saccular cavity. At the posteromedial corner the horizontal canal is connected with the marked swelling that represents an ampulla at the base of the posterior vertical semicircular canal. This is the largest ampulla of all three preserved, and anteriorly it joins via a large foramen into the posterior part of the superior sinus. This foramen provided entry for a ramus of the *accousticus* N VIII. The posterior semicircular canal that must have arched from this ampulla to the top of the superior sinus, would have been aligned at a low angle to the axial plane. The anterior vertical ampulla is connected with the horizontal canal as expected, and it also opens down into a foramen opening into the top of the sacculus. This must have carried a branch of nerve N VIII. As well as opening into the horizontal canal, this ampulla must have opened directly into the superior sinus of the saccular cavity, but this part of the specimen has been lost during preservation. We have reconstructed the canal so as to give a functional orientation with respect to the posterior canal.

The sacculus, which is exposed on both specimens, is large and has a convex well-rounded base extending ventrally to the base of the notochordal canal. The lateral wall has a very oblique surface sloping ventromedially at about 45°. The lateral margin is sharp and lies almost at the point where the jugular vein passes through the posterolateral wall.

Neither specimen has the anterior or posterior semicircular canals preserved, and we have no direct means of determining the height of the superior sinus. We do know, however, that the roof of the other dipnorhynchids is high and is supported from the braincase on a high median septum and two high dorsolateral septa. One skull roof of *D. kurikae* has the dorsolateral cristae partly preserved, and they are in a lateral position as in *D. sussmilchi* rather than close together as in *Chirodipterus australis*. This implies that the vertical space for the superior sinus or the space for the *ductus endolymphaticus* is large. Consequently we have restored these structures to the height implied by the space available from the horizontal structures that are preserved.

The only Devonian species with which a comparison of the labyrinth can be made are *Chirodipterus australis* Miles, *Holodipterus gogoensis* Miles and *Griphognathus whitei* Miles from the Late Devonian at Gogo, and *C. wildungensis* Gross from the Late Devonian of Wildungen. Säve-Söderbergh's (1952) attempt to understand the Wildungen specimen depended on his destruction of the specimen with a hammer and chisel. His illustration (1952: fig. 9, pl. 5,

fig. 4) of the otic region shows a clear outline similar to that given by Miles (1977: figs. 47–48), but the horizontal semicircular canal is not present on his photograph and is reconstructed on fig. 9. Despite this incompleteness, the two species of *Chirodipterus* are very close indeed. Neither of these species has the large ampulla on the posterior semicircular canal, the large utricular recess, and the laterally compressed horizontal canal, as found in *D. kurikae*. In *Chirodipterus*, the horizontal canal is semicircular in outline in dorsal view. *Holodipterus* is discussed by Miles and is said to be close to that of *Chirodipterus*. *Griphognathus whitei* has a similar arrangement to that of *Chirodipterus*, but its proportions are different because of the flattened shape of the skull. These differences are small in comparison with the obvious similarities between the species, and its occurrence in all the Devonian species in which the labyrinth is preserved, leads us to conclude that it is the primitive dipnoan pattern. Details of the comparison between the otic region of primitive dipnoans was discussed by Miles (1977: 98–103).

The nasal capsule

The capsule is preserved on the left side cf. ANU 48676, and is quite uncrushed. Miles (1977: 123) commented on the Gogo dipnoans that the surface of the neurocranium was evidently without a perichondral bone layer. The dorsal view of this specimen shows the junction between the dermal bone and the endocranium, and a perichondral layer lies around the endocranium (Figs. 3, 6A). We have also observed a similar layer in *C. australis*. The boundary between the neurocranium and the dermal bone is clearly outlined, and it is exactly like the boundary between the neurocranium and the dermal bone of the palate illustrated by Campbell & Barwick (1985: fig. 6d). The tubules over the top of the capsule, that is in the ethmoid capsule, were situated in a cartilage matrix (Miles, 1977: 133).

An internasal septum (*septum nasi*), is narrow and rather sharp crested towards the rear, but fades away almost completely anteriorly (Fig. 6B). It is formed of endocranial

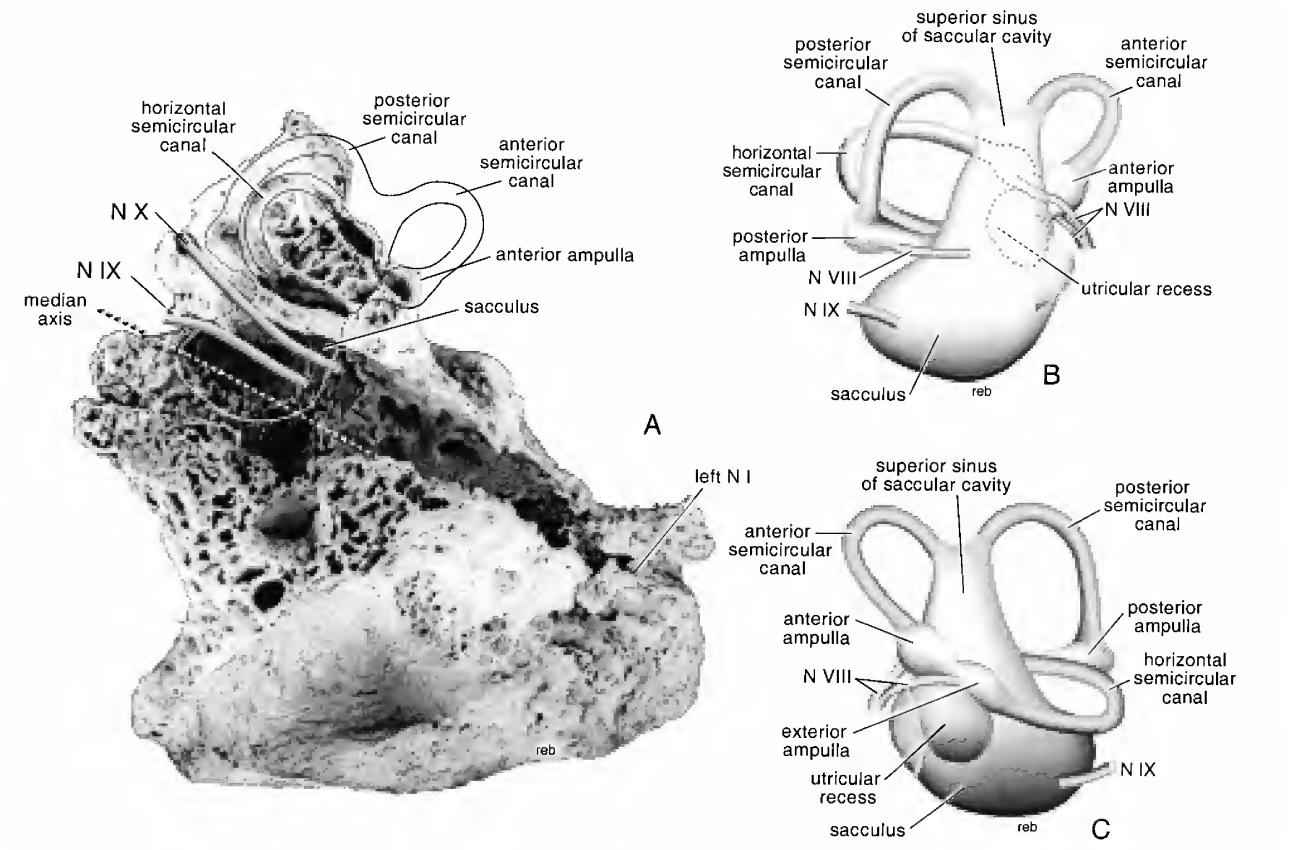

Figure 5. *Dipnorhynchus kurikae*. A—dorsolateral view of ANU 48678, the same specimen shown on Fig. 2. The semicircular canals were stripped off during preservation, but the details of the superior sinus of the sacculus, the ampullae of all three canals, and features more ventral to it are preserved. The height of the superior sinus is restored according to the height in the dorsolateral process supporting the braincase. The median axis is drawn along the base of the braincase. B—reconstruction of the left otic region viewed from the medial side. Outlines of structures on the lateral side are dotted. The same viewed from the lateral side. Nerve VIII is based on a canal and foramina in the specimen, and nerve IX is based on a foramen in the posterior wall of the specimen behind the sacculus. Scale = 10 mm.

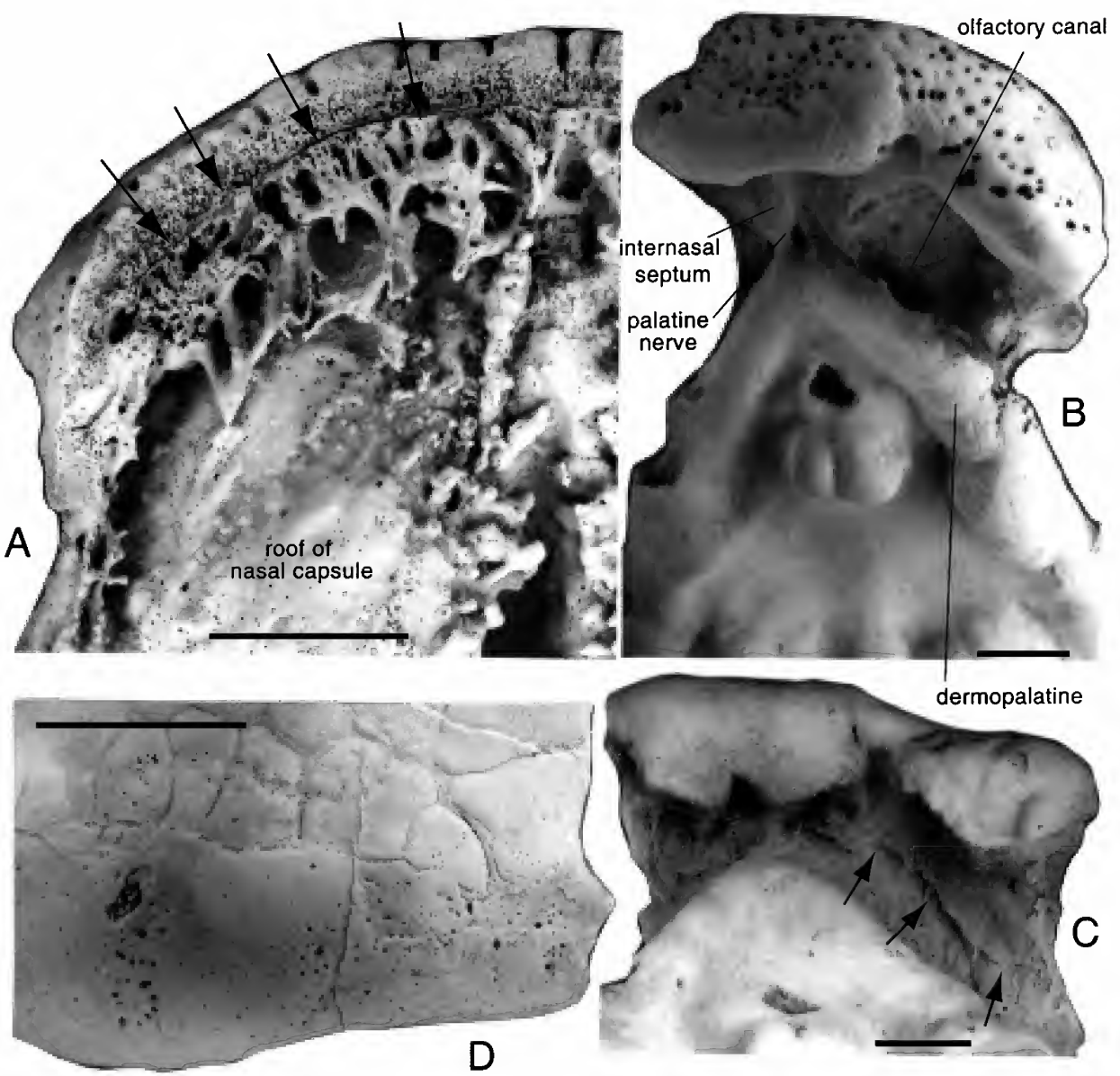

Figure 6. *Dipnorhynchus kurikae*, A–C from ANU 48676. A—dorsal view of the nasal capsule and snout, showing the dermal bone (innermost boundary arrowed) with pores in the outer layer, the gap between the dermal bone and the neurocranium with no tubules crossing into the dermal bone. The roof of the nasal capsule shows few structures because it was largely removed during preservation, and the black spots on it are bubbles in the impregnating plastic. B—view of the palate and snout with the snout tilted towards the observer. In the snout, note the pores some of which are in groups, the perforations for the palatine nerves, and the opening of the olfactory canal. C—same specimen tilted in the opposite direction, showing the flattened surface without pores on the inside of the snout, and the boundary (arrow) between the roof of the nasal capsule and the dermal bones of the snout (arrowed). D—*Dipnorhynchus sussmilchi*, anterior end of the snout of ANU 18815 showing the hard surface lying in front of the cosmine-bearing plates, the course of the lateral line canals, and the small pores on the anterior surface. Scales = 10 mm.

material, and its surface is smooth without any evidence that it continued ventrally as cartilage. Unlike *Chirodipterus australis*, it has no flattened surface to which a palatal bone (identified as a vomer by Miles) was attached. This is as would be expected, as the so-called vomer lies in a more posterior position between the dermopalatines in this species, and in comparison with *C. australis* the *septum nasi* certainly has a curious appearance (Miles, 1977: 134–135). Beyond its anterior end of the *septum nasi*, the edge of the anterior lip has a pronounced embayment within which is a foramen. This and foramina under the projections forming the embayment apparently connected with the tubules in the ethmoid capsule.

The nasal capsule is divided into three recesses (Fig. 7), which were discussed for *D. sussmilchi* by Thomson & Campbell (1971: fig. 29), whose terminology we use herein. The largest and deepest recess is posterior and it lies partly covered by the palate. The anteromedian recess is smaller than in *D. sussmilchi*, lies against the *septum nasi* medially and terminates against the anterior lip. The anterolateral recess is not sharply separated from the posterior recess, and anteriorly it runs up to the inner margin of the anterior naris. The anterior naris, which makes a deep recess in the anterior lip (Figs. 1A, 6B,C), connects with a shallow groove on the *solum nasi* which runs posteriorly across the anterolateral recess to the posterior recess. Miles (1977: 135) commented that he did not consider the threefold subdivision to be of significance, largely because no threefold division is present in *Chirodipterus australis*. On the other hand, it is present in *D. kurikae* in the same way as in *D. sussmilchi*, and clearly it is a feature of *Dipnorhynchus*. Bartsch (1993) commented that the outbulgings of the nasal sac present in early growth stages in *Neoceratodus* do not maintain their positions during ontogeny, and one suspects that outbulgings such as those in *Dipnorhynchus* represent the adult series of structures lost in later genera.

In dorsal view the olfactory tract has furrows in the surface indicating that the internal structure is complex. The olfactory tract expands in width and enters the posteromedial corner of the olfactory recess. In addition this recess is entered by two tubes, one lying close to the olfactory canal, and the other being a little more laterally placed (Figs. 3, 4A, 7). The former is much smaller than the latter, which is the opposite of the illustrated situation in *D. sussmilchi* (Thomson & Campbell, 1971: fig. 29). The interpretation of these canals is difficult, but we consider that the larger canal contained the *ramus maxillaris* N V_2, and the smaller one the *ramus ophthalmicus profundus* N V_1. The bone forming the roof of the nasal capsule is thin and was partly exposed by weathering. The exposed surface has numerous foramina which originally opened into the tubules in the ethmoid capsule. Thomson & Campbell (1971: fig. 29) show three canals running out of the dorsal surface and connected to the *olfactorius superficialis* N VII at the posterior end. We cannot confirm that a foramen for that nerve occurs in *D. kurikae*. However, two canals exit the capsule, one in a median position and the other laterally, at the front of the posterior recess (Fig. 1B). These canals join up with the tubules in the ethmoid capsule. Their connections are not clear.

Two other structures of consequence are present. The *palatine* N VII nerve exits from the palate in the appropriate position at the end of the palate. The groove for the subnasal vein (*maxillaris* vein of Miles, 1977) is in its usual position for Devonian dipnoans.

What appears to be part of the infraorbital lateral line canal runs along the lateral part of the specimen just dorsal to the edge of the labial pit (Fig. 1D). It is broken and cannot be traced around the anterior margin, though fragments are preserved. Anteriorly it is deeply buried in the bone and no exit pores have been observed. No part of the supraorbital canal is preserved.

The snout

An obvious feature of *D. kurikae* is large number of pores in the snout (Figs. 6A,B, 8A,B), these being more than three times the diameter of the largest pores in *D. sussmilchi*. The outline of the labial pit is preserved on the left side of the individual. It is much higher than the pit on *D. sussmilchi* (Fig. 1D). Both species of *Dipnorhynchus* have more laterally directed labial pouches which are more voluminous than those of *Chirodipterus australis*. This fits well with the fact that the mandible also has a large forwardly placed labial pit (Figs. 9C, 10A,B) that matches the large pit in the snout. The specimen also has the advantage of being weathered through the snout region so any interrelationships between the pores and the underlying bone can be observed.

Large pores are scattered over the anterior face of the snout, the largest ones being at the anterior edge (Figs. 1D, 6A,B). These reach a maximum diameter of about 1.5 mm. Some of them are not single units but are split internally into two or three elements. The smaller pits are limited in number to a few in a small cluster dorsal to the left nostril—they are only 0.3 mm in diameter. The returned margin of the lip, which turns back towards the nasal cavity, has no pores at all, and the small pits in this position on Fig. 7 are gaps in the impregnating substance. This returned surface is large in comparison with comparable surfaces on *D. sussmilchi* and *Chirodipterus australis*. Because it had distinctive bottom feeding characteristics with an extended bottom-feeding snout, *Griphognathus* had a much larger surface in this position.

At only one point, immediately dorsal to the labial pit, does the coarsely porous bone of the snout pass backwards into the pores of the cosmine surface (Fig. 1D). The boundary between the two types of surface is sharp, there being no place where the cosmine pores lie between the larger pores. On the other hand, the larger pores become smaller towards the cosmine, though they remain scattered and are still much larger than the cosmine pores.

The worn section across the snout (Fig. 6) shows several features that are distinctive. The outer layer, named layer 1 herein, is up to 2.5 mm thick. It is formed by columns of crystals with their long axes arranged normal to the specimen surface, and are separated by thin gaps—they can be observed by direct observation of the specimen, or by thin sections (Fig. 8). The hard material contains no dentine tubules, demonstrating that it is not dentine. The composition of the crystals will be discussed below. The crystals around each tube all go to cross-polar extinction in approximately the same position and there is little doubt that they are oriented in the similar direction. The space between the hard tissues consists of vertical calcite filled tubes. As can be seen in thin sections, these canals branch especially towards the outer surface. Despite this, the layer of tissue is hard and obviously withstood wear.

Inside this outer layer is a more vesicular bony layer, named layer 2 herein, which merges into layer 1. The boundary is clear at all levels of observation because in the inner layer the canals are more or less vertical, but are less regular in orientation and are more widely spaced (Fig. 8A,B,D). Some of the canals in this layer are continuous

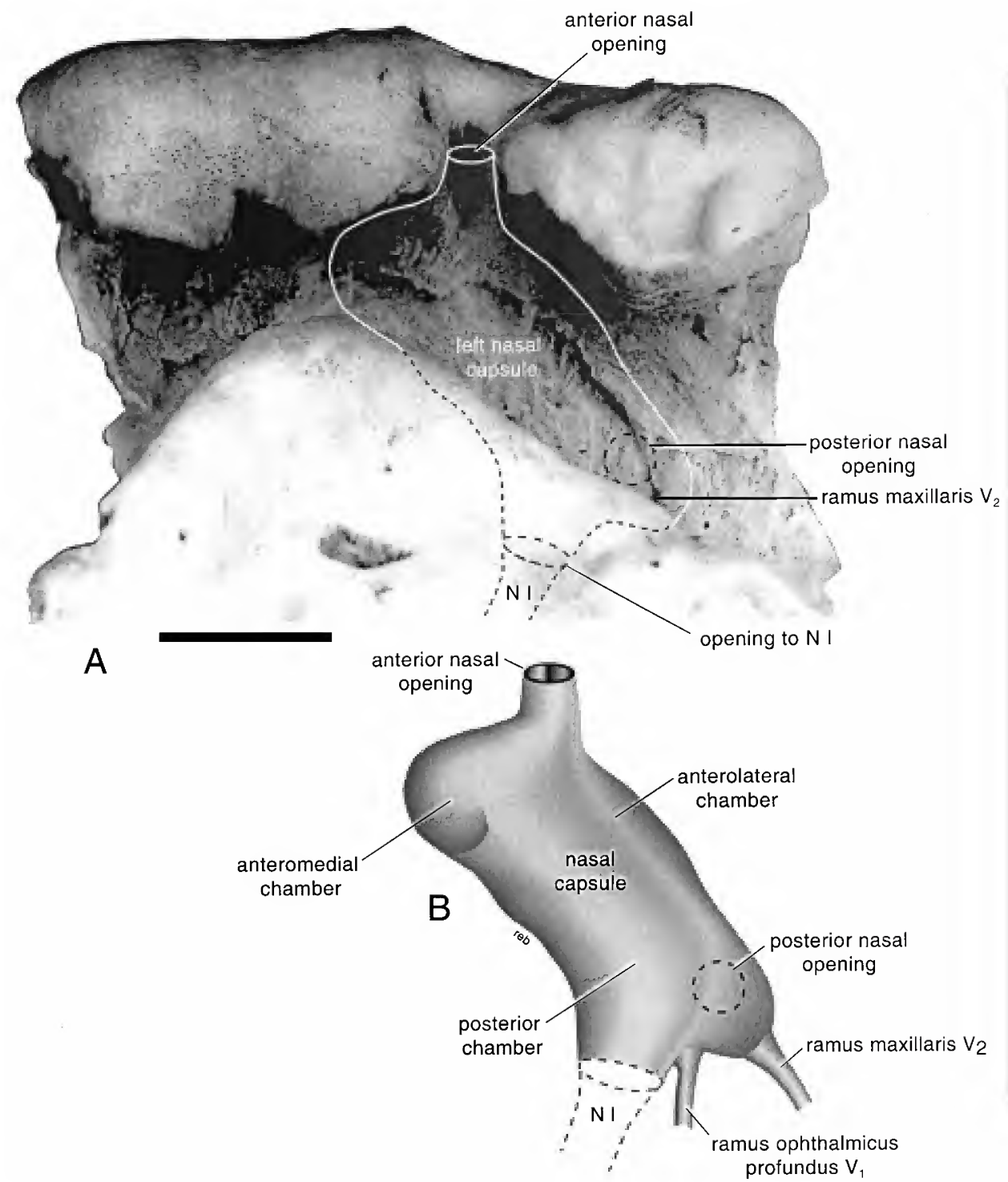

Figure 7. *Dipnorhynchus kurikae*. A—ANU 48676, tilted to the right, and with the anterior edge downwards. Outline of the nasal capsule inferred, and posterior nasal opening inferred from the shape of the dermopalatine. Position of the nerve N I observed and is so far under the palate because of the tilt on the specimen. B—reconstruction of the nasal capsule which does not have the strong subdivision as shown by Thomson & Campbell (1971: fig. 29), which was drawn from ANU 18815. Scales = 10 mm.

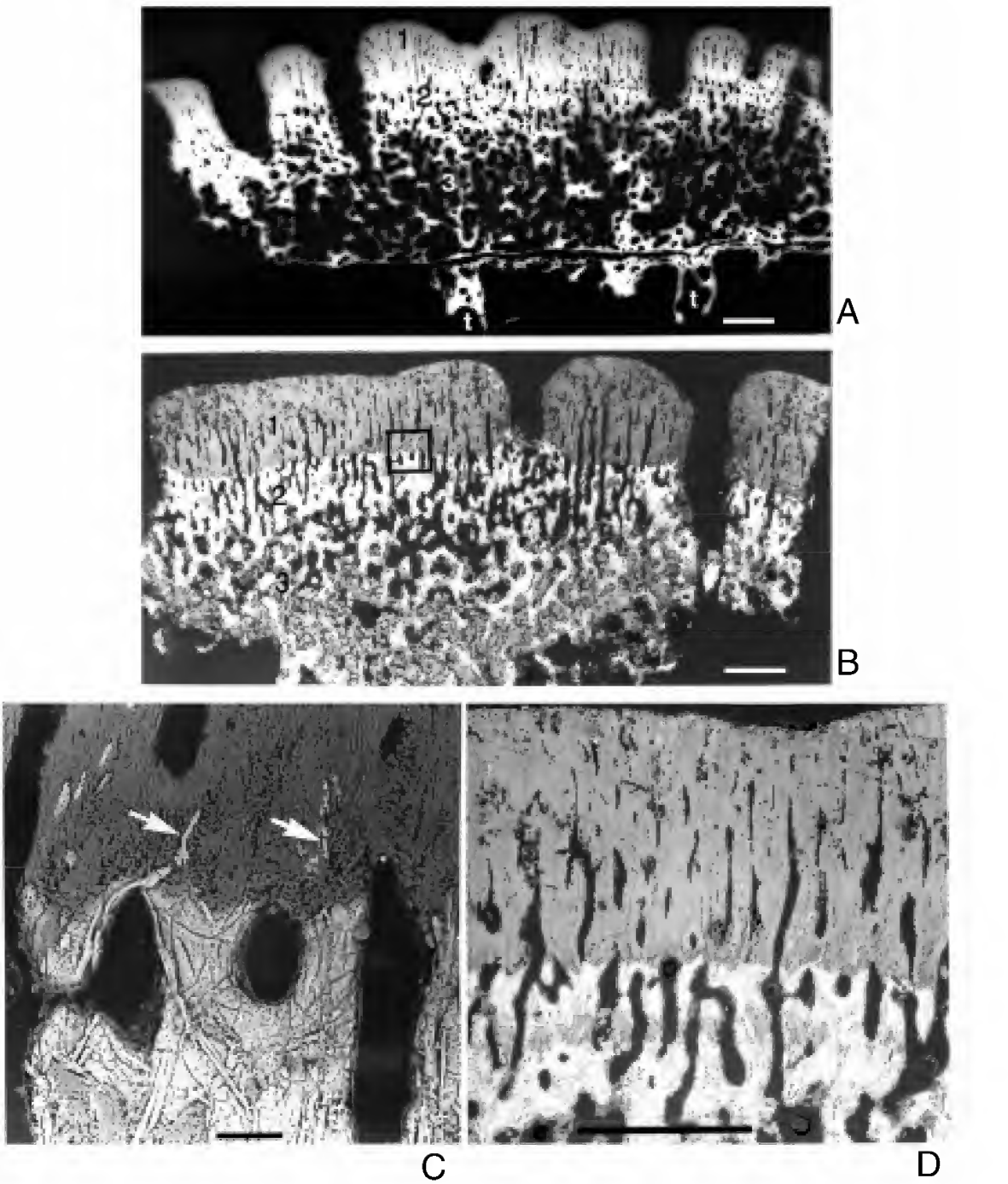

Figure 8. *Dipnorhynchus kurikae*, structure of the upper lip of ANU 48676 in both thin section and SEMs. A—thin section photographically printed directly from the slide, cut from the edge shown in Fig. 6A. Note the outer layer labelled 1, with its inner edge marked by a line of small perforations. Layer 2 has less regular canals and passes into layer 3 which consists of vesicular bone. The large outer pores vary in depth according to the orientation of the section. The boundary between the dermal bone and the neurocranium is marked by the two parallel bone layers. Fragments of tubules are labelled t at the base. B—SEMs of an adjacent layer which does not pass through so many pores. Layer 1 has a dark colour, the result of silicification, which was the result of preservation. Layer 2 shows many vertical canals passing into layer 1. The lower part of the section, including the lower part of layer 3, has calcite infilling. C—enlargement of the area in the rectangle showing crystals of fluorapatite at the base, and columns of quartz at the top. Note the fragments of apatite remaining in the quartz (arrowed). D—a wider area around the rectangle shown in B. Note the irregular arrangement of crystals in the lower columns. Scales: A, B and D = 1.0 mm; C = 0.1 mm.

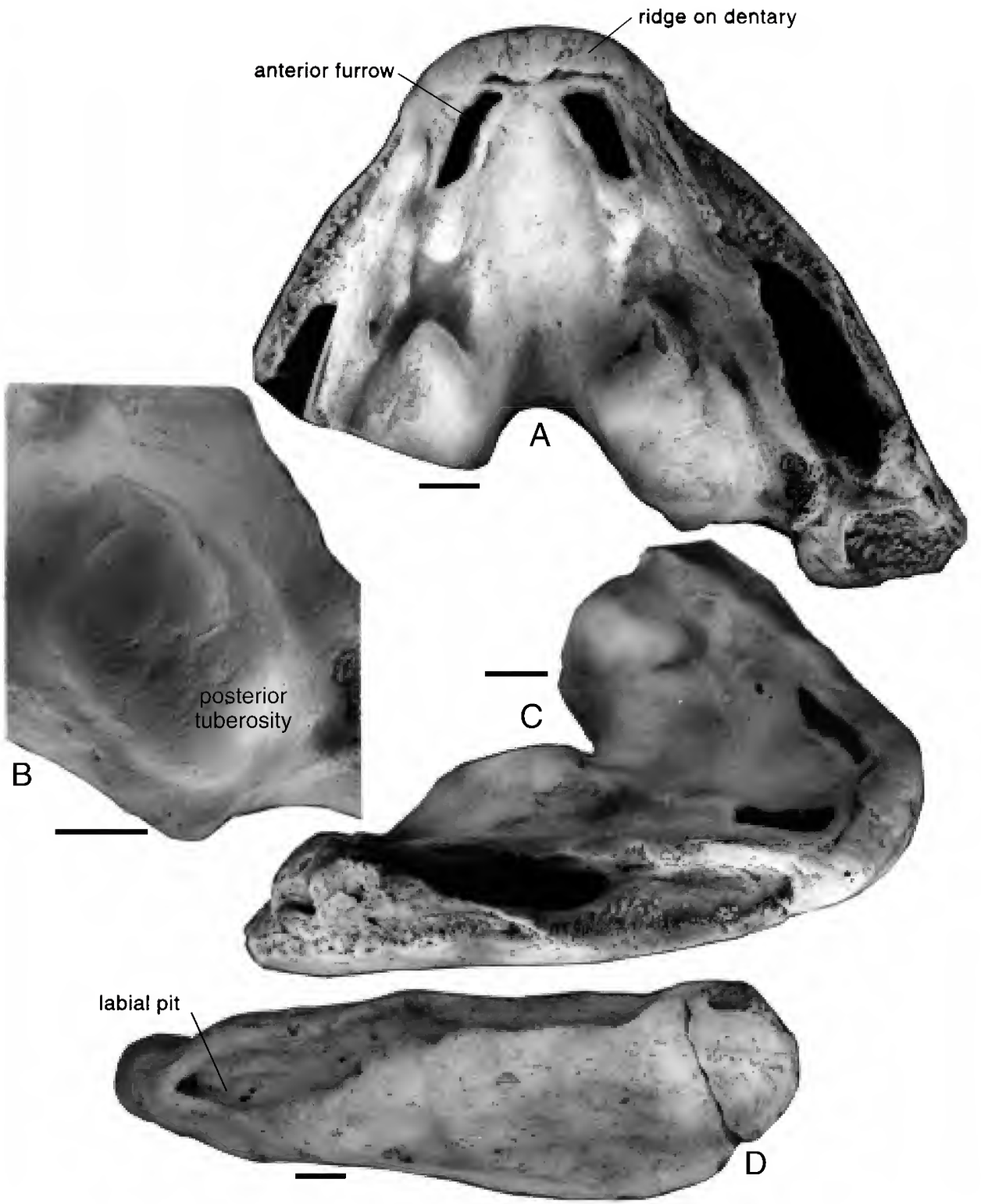

Figure 9. *Dipnorhynchus kurikae*, A–C from ANU 35643. A—dorsal view of a mandible from which the sections in Figs. 15A–C were cut. Note the shapes of the posterior tubercles, the glenoid fossa, the granules along the top of the surangular. B—an enlargement of the posterior tuberosity tilted to show the shapes of the different parts of the surface. C—anterolateral view of same specimen. Note the shape of the labial pit, the granules along the surangular, the low ridge on the dentary, and the rounded shape of the posterior tuberosities. D—lateral view of the ANU 60030. Other views as on Figs. 11, 12. Scales = 10 mm.

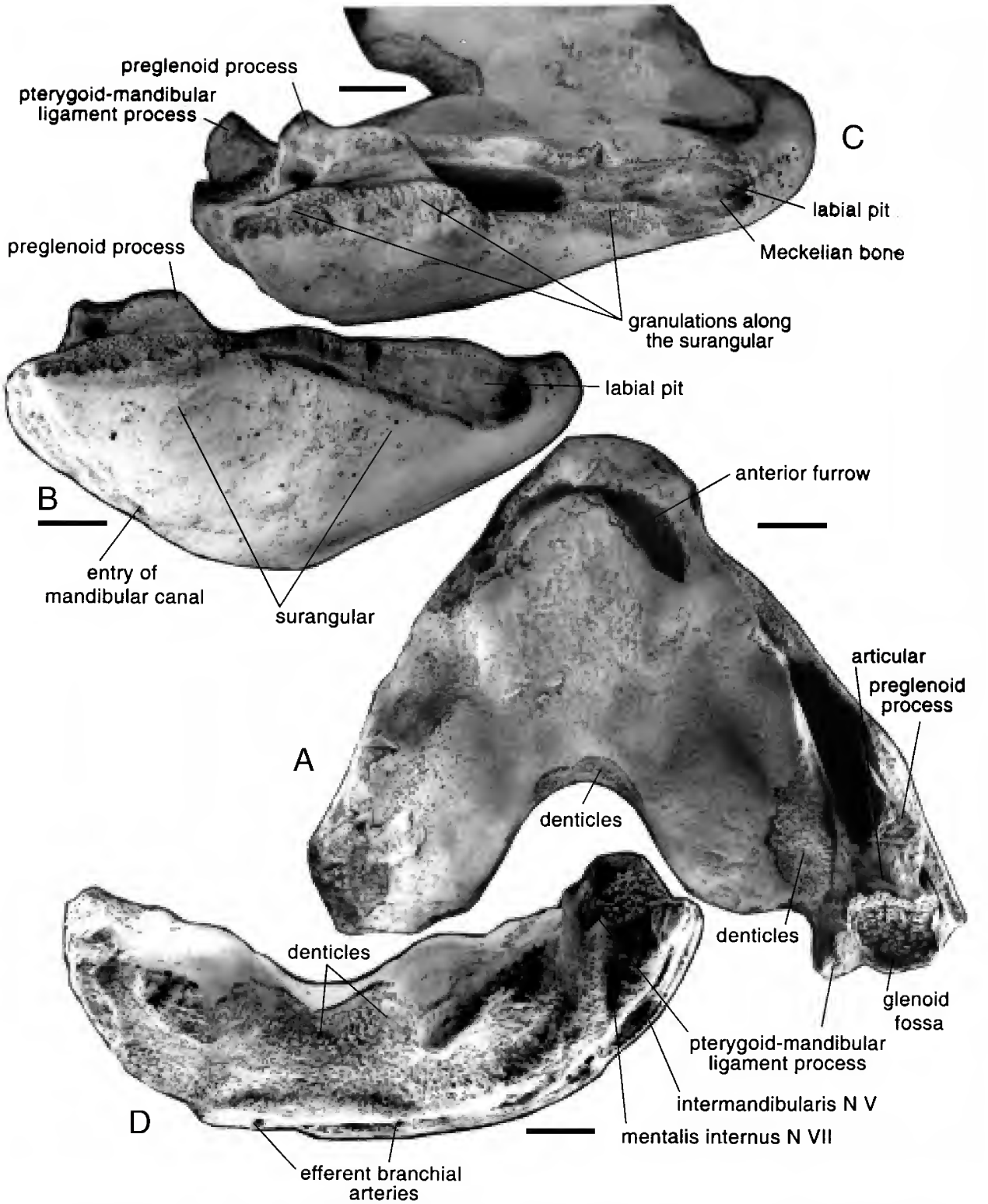

Figure 10. *Dipnorhynchus kurikae* ANU 60028; four views of a well-preserved mandible showing details of the right side clearly. A—dorsal view showing the slight secondary swelling of the glenoid fossa, and the preglenoid process. B—lateral view of same showing the large labial pit with the down-turned lateral edge on the surangular along its margin, and the denticles along the edge of the dental plate. C—oblique view of same showing the very high pterygoid-mandibular ligament, the large preglenoid process, the very high surangular along its lateral edge, the strong granulation along the surangular lateral to the labial pit, and the absence of large nerve pores in the posterior part of the pit. Note also the edge of the surangular and its junction with the outturned edge of the prearticular to form the base of the posterior part of the labial pit. Anterior edge of labial pit with pores in Meckelian Bone. D—posterior view of same showing the posterior end of the dental plate, the foramina for the nerve intermandibularis V; a groove running along the boundary between the articular and the prearticular and ending in the foramen for the mentalis internus N VII; and the foramina for the efferent branchial arteries symmetrically placed on either side of the mid-line. Scales = 10 mm.

with those in the outer layer. SEMs show that this layer is made of coarse crystals some of which are oriented normal to the surface, but others meet them obliquely (Fig. 8C,D).

Layer 2 merges gradually into layer 3 in which the vesicles are more equidimensional and the bone is more open. Internally the open spaces in the bone become more irregular, and its inner edge is formed of a very thin sheet of membranous bone.

The pores in the outer wall penetrate layer 1, and terminate within layer 2 (Fig. 8A,B). Those that terminate in layer 1 in thin sections appear to do so because of the obliquity of the section. No secondary pores have been observed entering the pores either at their base or laterally.

Inside these three dermal layers is a narrow gap bordered by thin membrane bones (shown by black arrows in Figs. 6A and 8A). Inside that are the branching tubules which are connected to the nerves V and VII which normally occupy tubules in the ethmoidal capsule. The tubules branch rapidly towards their termini (Fig. 6A), and they end abruptly against the gap between the membrane bones described above. Nowhere is there evidence that the tubules cross into the dermal layers, and neither is there evidence that the external pores in the dermal bones are in any way served by the nerves in the tubules.

From the external surface other aspects of the pores have to be taken into account. Some of them are not single structures, but consist of groups of two or three pores (Fig. 6B). Others are in small clusters. Finally as Figs. 8A and 8B indicate, the external entrance to the pores curve uniformly into the pores, suggesting that the soft tissues on the external surface dropped evenly into the pores.

Interpretation of dermal structures of the snout

The three layers described above are obviously parts of the dermal bone. X-ray diffraction study of layer 1 shows that it is composed of quartz and fluorapatite. The arrangement of these minerals is shown in Fig. 8C,D, and their distribution has several features of significance. The inner boundary of layer 1 is relatively straight against layer 2, and it crosses the vertical canals no matter what their orientations are (Fig. 8B–D). Sections along the boundary of layers 1 and 2 indicate that there is a sudden break between the tissues in any one column. Also included within this layer are crystals seemingly of material like that of the layer 2. From an optical mineralogical investigation and an SEM study of composition, we have concluded that layer 1 was originally apatite, but it has been replaced by silica, and fluorapatite. Immediately we are faced with the possibility that the replacement has removed dentine tubules, but we conclude that this is not correct. SEMs show no sign of the remnants of such canals, and the presence of cosmine pores in the adjacent surface indicates that fine structures have been preserved.

Analysis of layers 2–3 indicates that they are composed of fluorapatite, and the crystals are irregular in their orientation.

The external surface must have been covered with an epithelium, and the pores on the outer wall must have been filled with material related to the epithelial structures. Although the possibility remains of some fine connections with the internal layers, it is probable that the pores contained special surface structures such as mucous glands, and are not related in any way to endocranial tubules.

Other possibilities remain to be considered, largely following on the work of Bemis & Northcutt (1992), based on *Neoceratodus*. These authors also made comparisons between the *Neoceratodus* and some Devonian forms such as *Chirodipterus australis, Holodipterus gogoensis* and *Dipterus valenciennesi*. We are reluctant to make comparisons between *D. kurikae* and these species because the bone in their snouts consists of dentine in which the flask chambers of cosmine can be seen. There is no evidence that the dermal bone in these species has structure like that described herein for *D. kurikae*. In *Neoceratodus*, the dermal layer gives rise to dermal papillae and ampullary organs which are irregularly distributed. Neither of these features has the appearance or orientation of pores in the dermis of *D. kurikae*. Consequently we are not convinced that these features displayed by *Neoceratodus* can be appropriately recognised in *D. kurikae*.

We have also examined the two skulls of *Dipnorhynchus sussmilchi* available to us. The bone with the cosmine pores stop suddenly along a surface line (especially on ANU 18815), and anterior to that the bone is hard and contains no cosmine, but it does contain the pores for the lateral line canals (Fig. 6D). Larger more irregularly arranged pores occur across the remainder of the rostral area—they are quite comparable with the pores on *D. kurikae*, though they are much smaller. We have no explanation of the significance of size differences. It seems that the presence of pores is a characteristic feature of *Dipnorhynchus*.

The mandibles

External dermal bones. We now have four mandibles of the species, whereas at the time of original description we had one fragmentary individual, and another more or less complete one. With the specimens arranged so that the ventral median edge is horizontal, the smallest is 83 mm long, and the largest is 143 mm. The original specimen is 100 mm long, not 92 mm as stated in 1985. The range of sizes gives us an opportunity to discuss the ontogeny of the species. Now we describe the main features.

The mandible is low as is reflected by the posterior profile (Fig. 10D). The dentary increases in relative width compared to the total width of the specimen, being 0.27 in the smallest and 0.37 in the largest. Some specimens, especially one of the type specimens, have a shallow furrow on the ventral surface running transversely from the front end of the labial pit in an arc to the midline (Campbell & Barwick, 1985: fig. 8b). A complimentary furrow occurs on the other side. This marks the posterior edge of the dentary. Other specimens have a weaker furrow which is sometimes difficult to detect.

On the dorsal face of the dentary is a well-rounded ridge which is poorly developed on the smaller specimens but is high on the larger ones (Figs. 11A, 12, 13A,B). The ridge is not complete in all specimens, but in some it is divided into two or three irregular lobes (Figs. 9D, 13A,B). The best

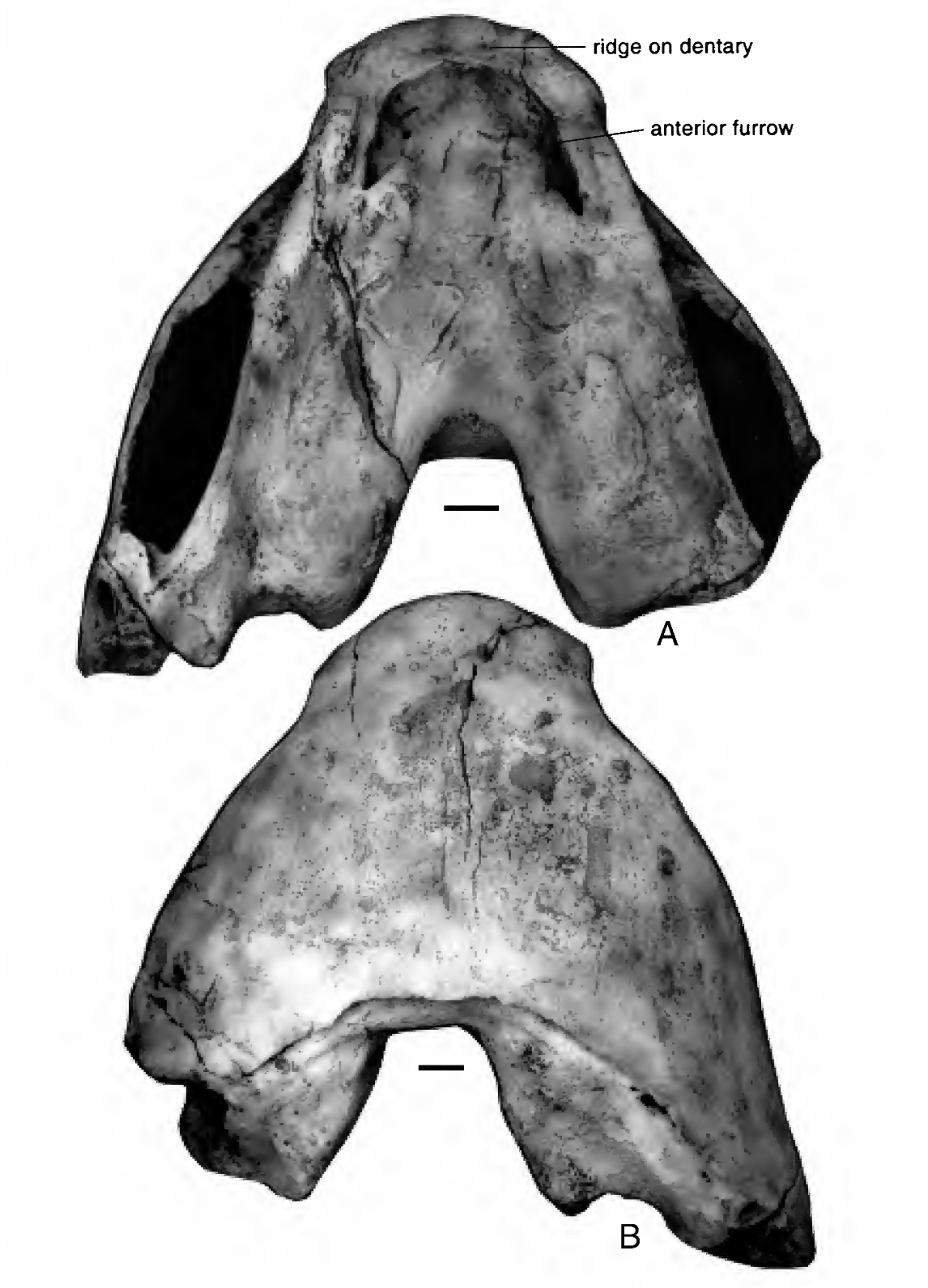

Figure 11. The largest specimen of a mandible of *Dipnorhynchus kurikae* known in ventral (A) and dorsal (B) views, ANU 60030. Details are labelled on Fig. 12. Note that the boundaries between the dermal bones are not clearly defined, but are overgrown by cosmine. Scale = 10 mm.

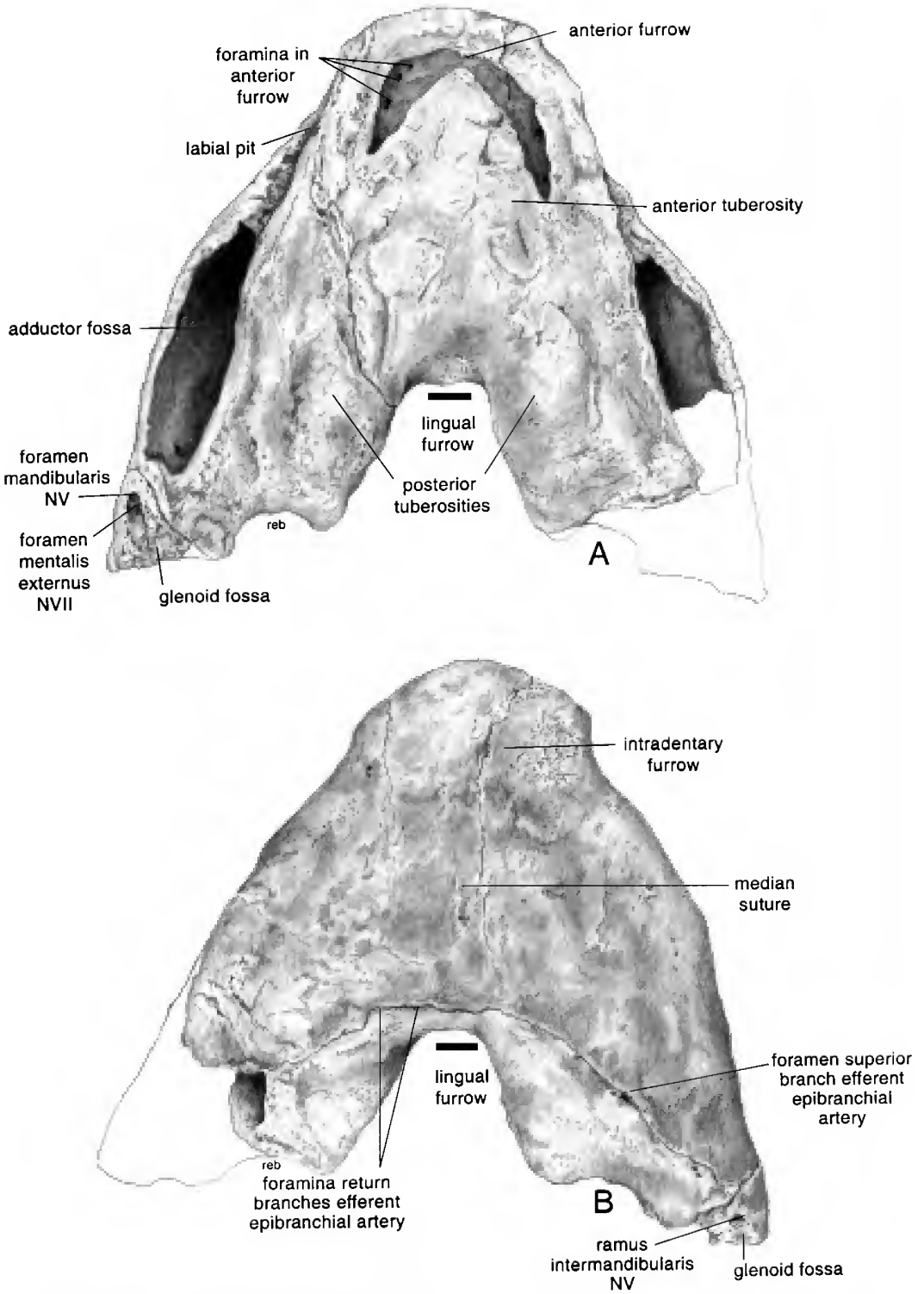

Figure 12. Illustration of specimen photographed in Fig. 11; ventral (A) and dorsal (B) views. Scales = 10 mm.

preserved individual has a break on its right side where the ridge becomes about half the height in the median portion. No pores like those of the surrounding dentary bones are present in the ridge. The edge of the ridge is differently developed on various members of the species. On ANU 60029 (Fig. 13A,C) both anterior and posterior edges are sharp, though the anterior one is less regular. The posterior edge is not straight but has small posteriorly directed expansions that overhang the dentary. What is more, the contact between the ridge and the dentary is exposed in places as a sharp line. The ridge must have been superimposed on the dentary. Because it becomes larger with age, the new tissue must have been deposited in layers, the mineralisation being supplied through canals running

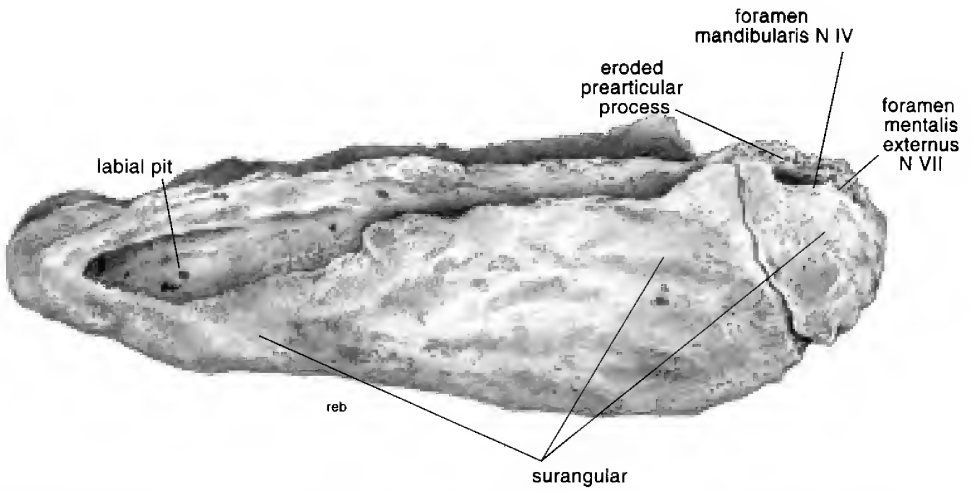

Figure 12 continued. Illustration of specimen photographed in Fig. 11; lateral view. Note that this specimen is depressed in relation to Fig. 10B.

up from the dentary. These canals can be seen in the ridge tissue itself, and it has been sectioned on ANU 60030 (Fig. 14). Details will be discussed below. The anterior edge on the same specimen also has a sharp edge laterally but the median part is broken. On *D. kurikae*, the dentary has no teeth such as those that occur on *Diabolepis* (Chang, 1995), in which the dentary teeth are of the same kind as on the prearticulars though they may not be in line with any rows of teeth on those bones.

The outlines of the infradentary bones are not clear on the specimens, but enough information is available to give a description of the main features. The surangular is a long bone reaching almost to the anterior end of the labial pit, where it comes into contact with the dentary. Its ventral edge is concave medially. Its posterodorsal surface against the articular is without cosmine and is covered with a fine granulation (Figs. 9A,C, 10A,B, 13C). Anteriorly its dorsal edge is inturned and is also covered with granules. It forms the outer half of the labial pit, but it is not upturned to form an outer raised rim to the pit. The posterior boundary of the angular is determined by the position of the mandibular lateral line entering the bone, but its anterior edge is not clear on the external surface of any specimen. Some details can be obtained from the internal view of the external bones provided by ANU 60029 which shows that the angular is a short bone that does not reach to the dentary, and from ANU 35643, which was figured in the original description. The postsplenial and the splenial are long bones which reach to the dentary. The postsplenial has a large lateral extension that turns around the angular towards the surangular ventral to the labial pit. The pattern of infradentaries is similar to that figured by Thomson & Campbell (1971: fig. 18A) for *D. sussmilchi*.

Anterior furrow. As with all other dipnorhynchids, the anterior furrow (Figs. 9A, 10A, 11A) is well developed. It extends extensively posteriorly, and in its floor are several foramina that open into the space ventral to it. We consider that this furrow, which contained well innervated soft tissue and is placed at the entrance to the mouth, is likely to have contained sensory structures (possibly chemosensory) related to food intake. *Chirodipterus* and probably *Dipterus* both have anterior furrows, and we consider that it is a feature of primitive dipnoans. The anterior furrow is not defined as a gap between the dentary and the prearticulars, but also as a space within which well innervated soft tissue was present. So far as we know, no such furrow which is innervated from the space ventral to it, appears in *Diabolepis* (Chang, 1995).

Labial pit. The labial pit is elongate and is bordered by the surangular. The dorsal edge of this bone does not form an upturned edge to the pit, but is bent downwards. As occurs in all dipnorhynchids, it joins the Meckelian bone to form the posterior floor of the labial pit. In *Chirodipterus*, the adductor pit is sealed off from the labial pit by the Meckelian and angular bones. *Dipnorhynchus* has a similar arrangement, though the surangular rather than the angular makes contact with the Meckelian bone. In both *Chirodipterus* and *Dipnorhynchus*, the anterior floor of the labial pit is made of Meckelian bone. In *Diabolepis*, the adductor pit is sealed off from the labial pit by the Meckelian and angular bones. *Dipnorhynchus* has a similar arrangement, though the surangular rather than the angular makes contact with the Meckelian bone. In both *Chirodipterus* and *Dipnorhynchus*, the anterior floor of the labial pit is made of Meckelian bone. In *Diabolepis*, the adductor pit is joined directly to the so-called labial pit (Chang, 1995: figs. 13, 14). The lateral margin is made of the dentary rather than the surangular or the angular, and so far as we know, the Meckelian bone is not directly turned laterally to form the base of the labial pit. In fact, the whole structure of the labial pit in *Diabolepis* needs further investigation, along with the so-called anterior pit, before comparison with dipnoans is attempted.

Dermal bones on the posterior face. These are well exposed on ANU 35643 and ANU 60028. Most of the surface is made up of the prearticular which is thick and has a rough surface. The articular bone does not have a sharp boundary with the prearticular, but it has an approximate boundary as shown on Fig. 10A. The foramen *intermandibularis* N V is in the usual position, and has a

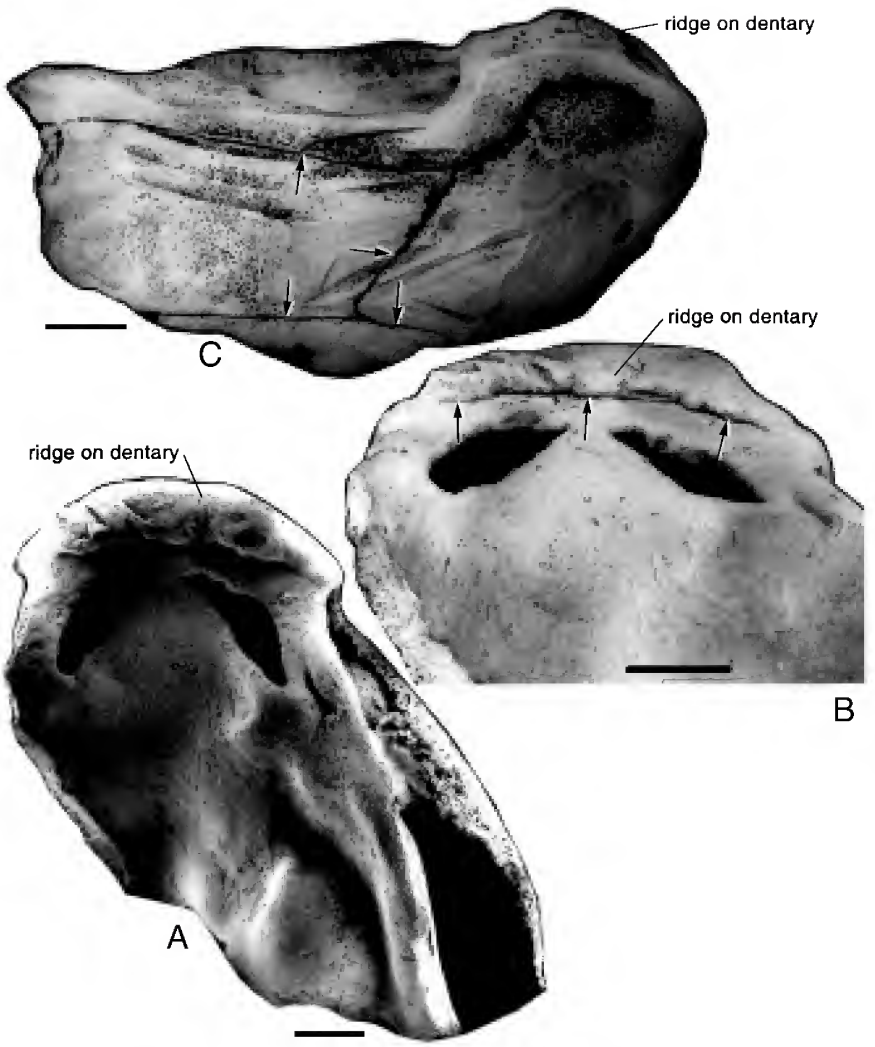

Figure 13. *Dipnorhynchus kurikae*, incomplete mandible ANU 60029. A—dorsal view showing the denticulated edge of the surangular along the edge of the labial pit, and the strong ridge along the dentary. B—posterior view of the dentary showing the nature of the overlap (arrows) area of the ridge on the dentary. C—ventrolateral view of specimen showing the lateral line canals (arrows) revealed by grinding the surface. Scales = 10 mm.

slight groove running both dorsally and ventrally along the boundary between the surangular bone and the articular. A small canal opens through the boundary between the articular and the prearticular medial to the *intermandibularis* foramen in the position illustrated by Thomson & Campbell (1971: figs. 21, 22) as f_1 sa1. This foramen has a vertical groove running into it dorsally. Internally its course can be followed along a canal on the inner face of the prearticular as shown by Thomson & Campbell as indicated above. We consider that it carried the *ramus mentalis internus* N VII. The canal labelled as fV? by Thomson & Campbell is also well shown on ANU 60028, and it rises up the back wall of the adductor chamber to meet the canals as shown by Thomson & Campbell (1971).

Large foramina occur between the angular and the prearticular, but a smaller one on ANU 60028. Unlike *D. sussmilchi*, it seems probable to us that several efferent branchial arteries entered the mandible here.

Lateral line canals. On an unprepared specimen the lateral line canal is difficult to follow, mainly because the pores are so small and difficult to pick up on the cosmine-coated surface. Surface grinding of the specimen ANU 60029 (Fig. 13C), and observation of other specimens, have exposed the position of the canals clearly. The oral canal runs along the surangular almost parallel to its upper cosmine-covered margin. Towards the anterior end of the labial pit, it curves forwards into the dentary. In its posterior course it is covered by a thin layer of bone, but further forward it sinks into the bone, and under the dentary it is more than 1 mm deep. The canal runs forward on the dentary and as it approaches the forward part of that bone it turns rather abruptly medially, and makes a shallow arc parallel with the anterior edge of the mandible. In this region the boundary of the canal is not sharply defined within the bone.

The mandibular canal enters the angular in its posterolateral corner and runs obliquely across the angular. It produces a transverse commissure on the postsplenial, and the long straight forward branch on the postsplenial is well exposed. This meets the oral canal ventral to the anterior end of the labial pit. The commissure is clear and it has a strong arcuate course towards the midline of the mandible.

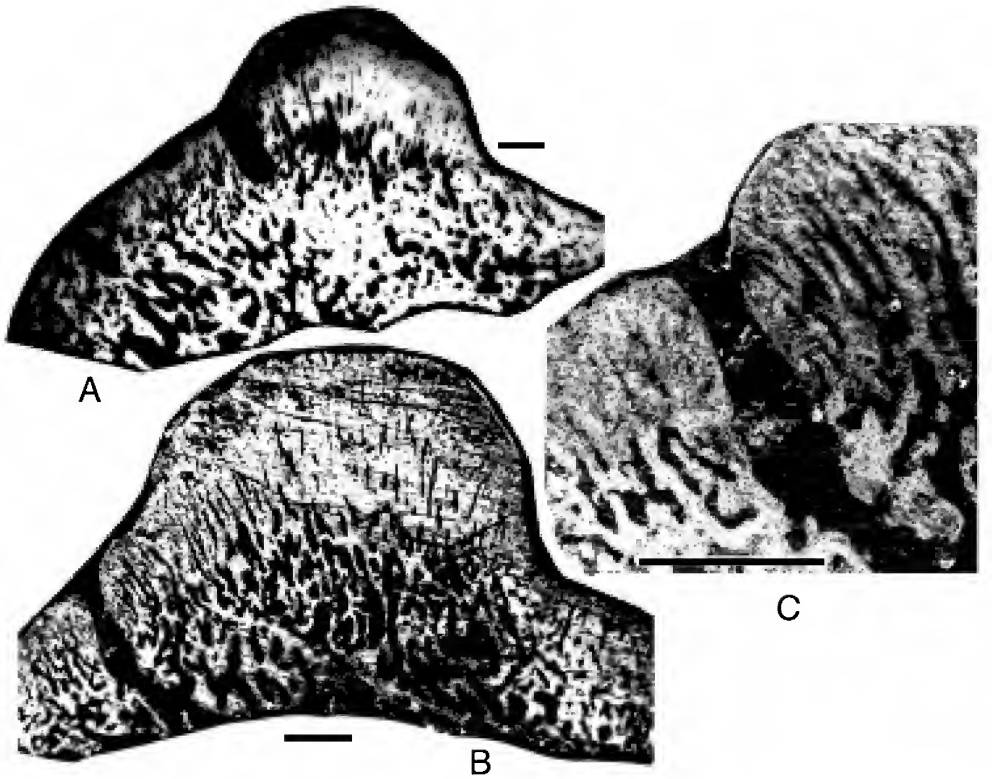

Figure 14. *Dipnorhynchus kurikae*, ANU 60030. Thin sections of the dorsal surface of the anterolateral part of the dentary of the specimen shown on Fig. 11. A—image of a section across the ridge on the dentary, produced by a direct photographic print of the section. The anterior edge is to the left, and the pores in the outer surface are the large depressions in the dentary. B—SEM section from the surface adjacent to A. Anterior edge to the left. The ridge is made of material with long canals which extend up from the dentary, the canals dividing towards the external surface, though this is difficult to see on the photograph because the specimen has been split by structural cleavage. The tissue of the dentary is largely vesicular, but it turns into more tubular canals towards the outer surface. C—left side of Fig. 14B, showing some detail of the microstructure, the detailed similarity between the tissue of the outgrowth and the dentary. Scales = 1.0 mm.

As would be expected because of the elongate middle section of the mandible, the posterior commissure is situated well forward of its normal position on later genera. It is 15 mm from the posterior edge in a mandible 50 mm in median length.

Comparison should be made with the canals on *Dipterus valenciennesi* (Jarvik, 1967: fig. 6) and *Chirodipterus australis* (Miles, 1977: fig. 102), both of which retain the primitive condition of four infradentaries. Nevertheless they have short surangulars, expanded angulars, and lateral line canals which almost run together in the angular. This is a derived pattern developed from the structures we have described for *D. sussmilchi* and *D. kurikae*.

Glenoid region of the mandible. The articular is well exposed on the original specimen described in 1985, and it is even more complete in ANU 60028 (Figs. 9A, 10A,B, 12A). The glenoid is a large structure which opens posterodorsally, and it has a slight flexure laterally, indicating a weak double joint. This is not nearly so pronounced as the lateral joint in *Chirodipterus australis* (Miles, 1977: fig. 104). Because it is open posteriorly the design of the joint does not provide a stable pattern for opening and closing the mandible, especially if large food items had to be processed. Two other features stabilise the joint. A posteromedial process has a dorsally projecting structure on the prearticular which is usually named the pterygoid-mandibular ligament process. It is often partly destroyed by wear, or it has a more flattened structure, but on ANU 60028 it is an elevated structure with a ligament attachment surface on its posterior face, and a separated scar on the anterior face (Fig. 10A,D). It may be that this process is unusually well developed on this one specimen, but it is so exposed that it could easily have been destroyed by wear on the other few specimens. This process is situated at the rear end of the glenoid, but would not be well situated to prevent posterior dislocation of the articulation.

The preglenoid process has a high rough surface on the articular standing 5 mm above the denticulated edge of the surangular (Fig. 10A–D). To this surface was attached a ligament or a muscle from the adductor chamber in the upper jaw. It is much stronger than the pterygoid-mandibular ligament, and probably was the main stabilising feature for the articulation. It is certainly in a position to help to arrest the posterior dislocation of the articulation. A similar, but smaller, process is present on other specimens of *Dipnorhynchus*, and on *Chirodipterus australis*, which also has an open posterior edge on the glenoid.

Adsymphysial region. We have four specimens of mandibles with the adsymphysial region preserved. Two of them have the anterior furrow divided by the prearticulars joining with the dentary and two do not (Figs. 9A, 10A, 11A, 12A, 13A). Examination of the former shows that the whole prearticular is extended forwards at depth, and the dentary is bent backwards to make the join which is solid bone. There is no indication that the connection is the result of a dental-plate making the join across a gap in the bone, unlike *Chirodipterus* which has an isolated bone lying across the anterior furrow nor *Holodipterus* which has a large plate wedged between the dentary and the prearticulars, but with a free base (Pridmore *et al.*, 1994). Nor is there any evidence that the anterior edge of the prearticulars in *D. kurikae* has sutures that could be interpreted as boundaries of an adsymphysial plate. Thomson & Campbell (1971: fig. 20) illustrated a structure labelled coronoids in this position, but its outline was indefinite and subsequent discoveries have convinced us that no separate bone exists in that position.

Clearly the presence of such a plate is not definitive of the Dipnoi, as it is absent in the primitive dipnorhynchids. Its origin remains a puzzle as although it is present in chirodipterids and holodipterids, it does not seem to be present in dipterids nor in rhinodipterids. It may be that it occurs as a neomorphic structure in several dipnoan stocks. So far as we can determine, no similar structure occurs in *Diabolepis*.

Prearticulars. These bones are very similar to those of *D. sussmilchi*, but the large tuberosities behind the anterior fossa are not connected back to the posterior tuberosities, and the transverse gap between the two is wide and shallow. Similarities that need to be emphasized are the patch of denticles at the corner inside the articular contact (Figs. 9A, 10A), the mass of denticles in the lingual furrow (Fig. 10A) and the posterior edge of the large posterior tuberosities. These leave a sharp edge on the tissue around the margins of the dental plate, indicating the backward growth of the plate.

The posterior tuberosities are not all of the same shape, some having the appearance of high rounded surface (Fig. 9A,B) and others being somewhat worn down. The high ones have one or two rounded furrows around them, the inner mounds being higher than the outer ones. This gives the appearance that the tubercles grew periodically during the growth of the animal. This would be a unique way for the dental plate to grow in a dipnoan, and it will be discussed below.

Growth of dental plates

We have to explain the growth of both upper and lower dental plates, as they are obviously complimentary structures. The dental plates of the mandible will be discussed first, and those of the palate will be discussed secondarily as we have less well preserved material available for sectioning.

Growth of the prearticular dental plates. White (1966) figured a prearticular tooth plate of *D. sussmilchi*, and commented that the blisters (tuberosities) were formed of a thickened layer of dentine continuous with the supporting bone. Denison (1974) did not place *D. sussmilchi* as part of his group with dental plates. He also indicated that its dental plates were covered with dentine, and commented that there is no evidence of how this dentine formed, or whether it continued to grow next to the spongy bone at its base as the buccal surface became worn. There are two main problems with these statements. Both authors accepted that the tissue forming the surface of the dental plate was dentine, although they could not understand how it formed; and secondly they assumed that the worn surface of the plates would remain worn because dentine could not be added to the surface once the original dentine had been deposited. These problems have been continued by subsequent workers who have assumed that dentine was present, though some workers have noted that the surfaces of the tuberosities were modified by later growth (Campbell & Barwick, 1985).

Not only has it been a problem with dipnorhynchids, but it has carried over into the understanding of *Speonesydrion* in which a bulbous mass of tissue forms the heel of the plates in the mandible (Campbell & Barwick, 1984; Smith, 1986). The more lateral parts of the plates in *Speonesydrion* have enamel covered teeth which have the usual dipnoan characteristics, even though the oldest parts of hard tissue lying on bone, and were modified by growth as in dipnorhynchids.

In *D. kurikae*, the left and right plates continue across the mid-line of the mandible without a break, and no mid-line suture is present. Consequently the dental plates cannot be added to by median growth along a suture, as is normal for dipterids, chirodipterids and later genera. We consider the dipnorhynchid pattern to be a primitive feature of dipnoans, and the development of the median suture appeared in the later Emsian probably in such genera as *Tarachomylax* Barwick *et al.*, 1997, and it became the means by which dental plates evolved by addition at the mid-line. Secondly the occlusal surfaces of the tuberosities are in some specimens rounded, as is shown by Figs. 1A, 9A,B and show no signs of wear. This occurs in both the large posterior tuberosities and the smaller anterior ones. The surfaces of some tuberosities are not smooth, but show grooves which are subconcentric or irregular in their distribution (Fig. 9B). In the mandible the central part of the tuberosities is highest and well rounded indicating that it was the most recently added sector. Obviously the tubercular part of the plate did not increase in size laterally as they did later dipnoans, nor did they modify their shape in the oral cavity by growth at the plate margins. Yet they did increase in size during growth of the animal, as did the marginal ridges.

A thin section of the large posterior tuberosity on the mandible is illustrated in Fig. 15. It also shows the thick bony layers of the tuberosity in which the growth took place at different rates and produced the shapes shown externally in Fig. 9B. It also shows the thin layer of surface tissue (dentine) in which the canals are vertical to the tooth-plate surface. In particular, we illustrate the surface between the tuberosity and the marginal ridge in which the surface layer is well preserved (Fig. 15A–C). It was by the resorption of this layer, or by the addition of new canals between the original ones, which allowed the shape of this part of the plate to change during growth. Detail of this layer is shown on Fig. 16A, in which the vertical columns of dentine are still visible though some post-mortem changes have taken place. The marginal ridge is not well preserved in the thin

Figure 15. *Dipnorhynchus kurikae*, sections across the posterior tuberosity of ANU 35643. A—an almost complete section, lateral ridge (slightly incomplete) to the left and the lingual surface to the right. The dark coloured material on the dorsal surface is the tissue was added to at its junction with the adjacent bone during the growth of the plate. The gap in the centre is the result of loss during grinding. Compare with White (1966: pl. 1, fig. 1). B—enlargement of the lateral ridge and adjacent surface. Note the thin dark layer on the surface, the underlying tissue with elongate columns, and the thinning out of the surface tissue in the groove. Note the thin layer of fine texture on the surface on the left side. C—section cut adjacent to A and B, but with the marginal ridge well preserved, though broken across. Note the elongate tubes forming the bulk of the marginal ridge and the way it dies out laterally against the prearticular. Scales: A = 10 mm; B–C = 1.0 mm.

sections, but the canal-like tissue thickens into the ridge on its medial side but laterally it thins out onto the prearticular. An enlargement of the outer surface of the posterior tuberosity outlined on Fig. 15A, is given in Fig. 16B. This shows the columns of tissue growing upwards from the prearticular. On the outside surface of the bone is a very thin layer of harder tissue, only 0.3 mm thick. This thin layer also occurs on the tubercle although it is not so well shown on the photograph. The continuity of this layer across the whole dental surface indicates that it was formed from a layer of surface tissue which originally covered the dental surface, or by modification of the ends of the bony columns underlying it. The first suggestion requires the covering of the dental surface at sites which are active in biting, and scarcely seems a possibility. We prefer the second view, but do not have an explanation of the process involved. The section also shows some thin horizontal tubes which are the result of post-mortem effects.

The arrangement of the bony tubules in the space between the tuberosity and the marginal ridge, must have been the result of resorption of bone and the deposition of new bone at specific locations. As indicated above, this is well illustrated by Figs. 15, 16 and 17, which also follow the pattern illustrated by the overgrowth on the dentary as in Figs. 14A–C (see discussion below). This process may cause difficulty in interpretation of the growth process but, given our observations, we can see no alternative.

The lateral and posterior margins of the prearticular plates show no increase in the wear surface of the tooth plate except for the small denticles around the edge of the plate. These denticles are overgrown by extension of the continuous tooth plate tissue over the tubercles. This allows the marginal ridge to be modified in shape, and the form of the lingual cavity in the mandible to be modified with further growth.

All the above points indicate that:

1 plate growth did not take place by the addition of marginal growth in the form of teeth as in other dipnoans;
2 plate growth did not take place by the addition of new layers of tissue at the mid-line, nor did resorption of the plate take place at the mid-line of the palate or the mandible;
3 there are no homologues of real teeth in the system;
4 the marginal ridges were added to by resorption at their inner edges, and the deposition of new bone to expand the ridges and the inner face of the palate or the prearticulars;
5 lateral growth of the plates in both jaws took place by the overgrowth of the small denticles around the plate margins, and posterior growth by similar overgrowth on tubercles in the labial cavity;
6 vertical growth of the plates in both jaws must have taken place by the upward growth of the tuberosities and the surface tissue between them by differential bone growth from within the plate tissue, and addition to the base of the dentine layer;
7 this whole pattern of growth is completely different from any other dipnoan, and in our view represents a first step towards development of palatal biting by dipnoans, one of the most distinctive features of the group.

The understanding of this type of growth is provided by the outgrowth on the dentary which is so well shown on ANU 60029 and ANU 60030, and illustrated on Fig. 14. To check these points it is necessary to prepare thin sections of the material to examine the structure of the tissue.

Thin sections of the ridge on the dentary of ANU 60030 show some geological structural cleavage, but the biological structure remains clear. The bone of the dentary is vesicular. It passes over a roughly defined boundary into vertically organised tissue through which long tubes extend to the external surface. Although many canals are continuous, others are branched. Towards the edge of the ridge the canals bend towards the margin of the ridge, and merge with the pattern of the canals in the dentary. The hard tissue must have been laid down around the individual tubes, the tissue around adjacent tubes meeting at a dark line in vertical section. The internal structure of the hard tissue is homogeneous. No dentine tubules are present within the tissue.

The deposition of this ridge tissue is a matter of major concern. No sign of the original surface of the dentary under the ridge is preserved. It must have been resorbed and new coarse vesicular bone tissue was deposited extending up into the base of the ridge during growth. The ridge itself contains elongate tubes which reach to the surface, and this would have been deposited by mineralisation transmitted through the older bone beneath. In summary then, the depositional process involves the modification of the older bone, its replacement by new vesicular bone and the growth of new vertically arranged bone around the outer surface. The fact that the materials are all bone and no dentine is involved, accounts for the absence of a pulp cavity and the lumpy arrangement of the ridge tissue, points which both White (1966) and Denison (1974) were unable to comment upon. This pattern provides the basis for the interpretation of the periodically growing bone-based dental plates.

The mandibular structure of *Diabolepis*, with its prolingual field, a short symphysis, and a median gap which opens easily to allow the two halves of the mandible to be preserved

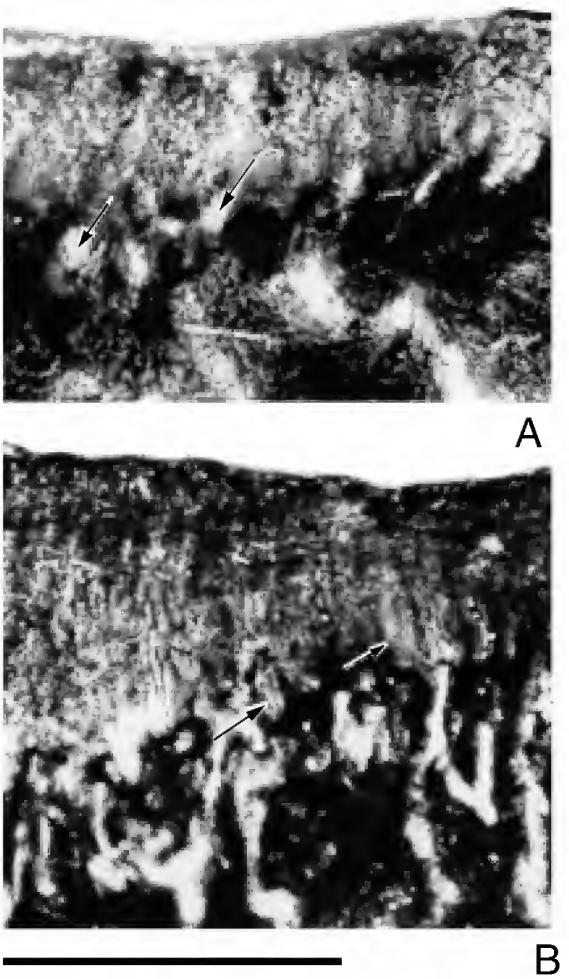

Figure 16. *Dipnorhynchus kurikae*, thin sections of ANU 35643 photographed to show detail. The specimen was slightly altered during preservation, and some of the detail has been lost. A—surface tissue in the valley between the posterior tuberosity and the lateral ridge, indicated by an arrow in Fig. 15A. The external layer shows traces of columns of bones (arrowed) lying on coarsely vesicular prearticular. B—section of the posterior tuberosity as marked on Fig. 15A. This shows more clearly the structure (arrowed) of the surface tissue. Vesicular tissue in the lower parts of the sections. Scale = 1 mm.

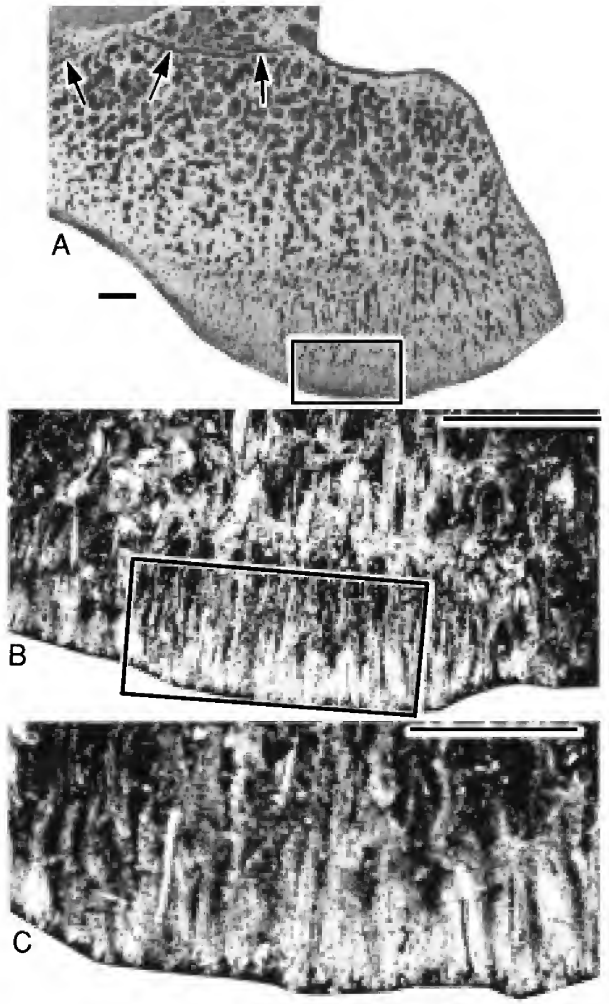

Figure 17. *Dipnorhynchus kurikae*, sections across the anterior palatal tuberosity of ANU 36508, figured by Campbell & Barwick (1985: fig. 6d). A—direct photographic print from the section. The boundary between the pterygoid and the neurocranium is shown by arrows at the top. B and C are printed from negatives made from the palatal face of the above section. B is from the area of the rectangle in Fig. 17A, and shows the tuberosity near the base. The coarse tissue at the top of the photograph corresponds with the coarse tissue between the fine tubular tissue and the coarser tissue against the vesicular bone in Fig. 14A. C—enlargement of the rectangle in Fig. 17B, and shows the tubes towards the biting surface. No dentine tubules are visible. Scales: A = 10 mm; B = 0.5 mm and C = 0.25 mm.

separately (Chang, 1995), has nothing similar in structure to this pattern whether one agrees with its interpretation or not.

Growth of the palatal dental plate. The only palate we have for sectioning is ANU 36508. Its surface has been subjected to wear during preservation, and so the grinding surface has been removed. However, enough tissue is preserved on the anterior tuberosity to prepare a study of the histology. A section across this part of the plate was figured by Campbell & Barwick (1985: fig. 6d). The tuberosity on the right of that figure is also refigured herein (Fig. 17) at larger magnifications to show the detail of the canals. The specimen has a large number of post-mortem borings through the bone, but the details remain clear. The canals and the hard tissue are almost identical to those described above for the ridge on the dentary. There is no sharp boundary between the pterygoid bone and the tissue making up the surface of the lateral tuberosity. As can be seen from the figures mentioned above, that tissue consists of columns like those on the surface of the prearticulars. This dentine-like substance is without dentine tubules, and is connected with the adjacent bone without any sign of a pulp cavity. This arrangement makes it possible for the bone making the tuberosity to increase in height by addition to the bony base. Such an arrangement will permit the bulbous surfaces on the palate to develop during growth. We do not have a good section through the posterior tuberosity, but the ends of the canals are well exposed on the layer illustrated by Campbell & Barwick (1985, fig. 6b). This demonstrates the point that the same material occurs across the whole palatal surface.

Conclusions

New discoveries of topotypes of *Dipnorhynchus kurikae* have allowed us to describe a braincase which has been exposed by etching. This is the first braincase of an Early Devonian dipnoan described from an exposed internal and external neurocranial walls, and a moderately exposed otic region. Previous descriptions by Thomson & Campbell (1971) and Campbell & Barwick (1982) were based on external structures of the neurocranium. The similarity of the braincase to that of the extant *Neoceratodus* is striking, and the identification of the various nerves is made without difficulty. In particular, the recognition of the lateral line nerve is clear. The pattern of the elements of the braincase were established early in the evolution of the dipnoans, and subsequent changes have only modified the proportions of this basic pattern.

The second major feature of this material concerns the dental plates. These include large tuberosities and marginal ridges, the cores of which are bone and the surfaces carry thin layers of dentine which contain no dentine tubercles. Because of this, the shape of the palatal surface was changed by new growth of bone, making growth layers of different heights on the tooth plate surface. This is a major feature of dipnoan evolution, because *Speonesydrion*, which has real enamel-covered teeth around the anterior and lateral margins of its tooth plates, begins growth with featureless plates lying on bone, and then adds enamel-covered teeth at a later stage of ontogeny (Campbell & Barwick, 1984). *Speonesydrion* has the other characters of a primitive dipnoan, as outlined by Campbell & Barwick (1987). The appearance of tooth-plated dipnoan genera in rocks older than those containing *Dipnorhynchus* has not been established, though some workers wish to have *Diabolepis* as an early dipnoan. We do not accept this, and point out the difficulties involved with that hypothesis in a paper submitted for publication. Recent papers dealing with *Diabolepis* were primarily concerned with the early evolution of sarcopterygians, and were not specifically concerned with dipnoans. The differences of opinion are illustrated by reference to work by Cloutier & Ahlberg (1995, 1996) and by Zhu & Schultze (1997). In our view, *Diabolepis* is more closely related to *Youngolepis* and *Powichthys* than it is to dipnoans.

Thirdly, sections of the upper lip show a pattern of growth in which an outer layer of bone with elongate canals and

contains large foramen which do not connect with the rostral tubules in the ethmoid capsule, a second layer of bone in which the canal structure is more diverse, and a third layer in which the bone structure is vesicular. This is separated off from the endocranium by a distinct gap. This is probably a distinctive primitive feature of dipnoans as it is also found in *D. sussmilchi*, though no sections of that species have been cut (Thomson & Campbell, 1971: fig. 57).

The lip structure of the species is of importance because of the fact that dipnoans use their lips as part of the buccal suction pattern of feeding. The description of the lips of *D. cathlesae* (Campbell & Barwick, 1999) indicates the extent to which the early dipnoans had lip structures which we interpret as capable of producing a strong suctorial capacity, and *D. kurikae* is the next oldest species with which it can be compared. The lip structure of *Diabolepis*, in so far as it is known (Chang, 1995), is totally different in its disposition.

The presence of an anterior furrow in *D. sussmilchi* is shown to be a feature in *D. kurikae, D. cathlesae, Speonesydrion iani* and *Uranolophus*, and it seems to have been an important feature of primitive dipnoans. It contained soft tissues richly innervated from a ventral direction and so must have contained a sensory system of some kind. So far as we can establish, it does not occur in *Diabolepis*, where there is only an interface between the dentary and the prearticulars. No Early Devonian dipnoan in the NSW sequence has any indication of tooth bearing structures labelled as prolingual field in *Diabolepis*. Finally, the vomers and the labial pit in *Diabolepis* are not of the kind found in the Early Devonian dipnoans. We conclude that *Diabolepis* is not related to the genera which gave rise to the Dipnoi, but is a side branch related to *Youngolepis* and *Powichthys*.

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